ENERGETICS AND SPACE USE OF FEMALE MOOSE DURING WINTER

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Abstract

Space use and resource selection are processes linked by habitat availability that have direct consequences to fitness. Knowledge of such processes allows comprehension of wildlife-habitat relationships, which can improve the efficacy of wildlife management programs. I investigated energetic and space use parameters of a population of female moose wintering in two adjacent, but distinct, landscape types (lowlands and mountains) on the Kenai Peninsula, AK, USA. I also evaluated differences between four home range models. I found that mountain females started winter in better condition, but used fat reserves at a higher rate than lowland females resulting in similar body condition estimates of moose in both landscape types in spring. I also found evidence of the functional response of habitat selection at the home range scale within landscape types. I observed a strong positive correlation between daily movement rate and home range size indicating that when females move during winter, they do so to access new areas expanding their home range. Brownian bridge, minimum convex polygon, fixed kernel, and local convex hull home range models produced different area and overlap estimates. Minimum convex polygons are least similar of model types and are not recommended to estimate areas actually used by animals.

Dedication

This thesis is dedicated to my grandfather, Robert G. Wright, patriarch of our family. He played a large role inspiring me to appreciate wildlife and the places they live. He passed in Colorado, while I was completing my research in Alaska.

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Chapter 1 General Introduction

As the human population increases, wildlife resources per capita decline. Therefore, more informed management strategies are required to sustain wildlife populations and the variety of uses desired by the public. Wildlife management programs not based on accurate ecological knowledge, can, and have, produced population responses that under- or overcompensated management goals (Boertje et al. 2007). Such undesirable results can lead to confusion and ultimately distrust by the public (Mackie 2000). Today, the public, non-government organizations, courts, and various legislative factions scrutinize management actions by wildlife professionals. Therefore, responsible wildlife management must be based on sound ecological knowledge and able to withstand the rigors established by courts of law. Monitoring population responses to variations in limiting factors can provide more robust management programs through better ecological understanding (Dussault et al. 2005).

Moose (*Alces alces gigas*) management on the Kenai Peninsula, Alaska, USA, is no exception to the above statements. An increasing resident and seasonal human population impact moose and other wildlife throughout the peninsula. Questions of how to properly manage Kenai moose populations have been a concern since the early 1980s (Bangs et al. 1982). This management concern is genuine because of the importance of moose as a renewable wildlife resource and recently documented habitat

changes on the Peninsula (Klein et al. 2005). Moose are valued due to their importance as a food source, the opportunities they provide for tourism and recreation, and their role in ecosystem function (Timmermann and Buss 1998). Impetus for this research stems from the desire to gain needed ecological knowledge of moose-habitat relationships in order to better manage moose populations. Specifically, local wildlife managers were interested in investigating differences in energetics and space use among moose inhabiting different habitats. Habitat is defined throughout this thesis in the multidimensional sense to include all resources (e.g., forage types and shelter) and environmental conditions (e.g., precipitation and snow depth; Gaillard et al. 2010).

On the Kenai Peninsula, moose winter in mountain and lowland landscapes. These landscapes are composed of different vegetative communities and environmental conditions. Evaluating moose energetics can provide insights into fitness and habitat quality differences between the two landscape types and the adaptive capacity of moose. Habitat evaluation could also help managers establish management regimes.

The space use parameters home range size and daily movement rate have the potential as indicators of habitat quality. However, there is debate in the literature over the use of space use parameters as metrics of habitat quality (Dussault et al. 2005, Reid et al. 2007, Herfindal et al. 2009, Linklater et al. 2010). The proposed metrics are the result of a corollary of the home range size hypothesis (Burt 1943), which states that home range

size and movement rate are negatively related to habitat quality (Harestad and Bunnell 1979, Dussault et al. 2005). Therefore, a negative relationship between home range size and daily movement rate with habitat quality is expected. However, in order to use home range size and movement rate as habitat metrics, the energetic requirements of the study animal must be accounted for (Burt 1943, Harestad and Bunnell 1979).

While evaluating cow moose energetics and space use I found a strong positive correlation between home range size and daily movement rate. Foraging ecology theory advocates such a relationship during winter (Owen-Smith et al. 2010). To be certain this relationship was not an artifact of the type of home range model used during the study (Brownian bridge movement models (Horne et al. 2007)), I used the three additional common home range models minimum convex polygons (Mohr 1947), fixed kernels (Worton 1989), and local convex hulls (Getz et al. 2007) to evaluate the correlation. Like many researchers before me, once I had constructed home ranges from four different model types, I could not resist the urge to compare the differences between the home range model types constructed. Home range size and the degree of spatial overlap are good evaluates of home range models.

The objectives of this research were to:

1) Determine the energetic consequences of cow moose wintering lowland and mountain landscapes on the Kenai Peninsula.

2) Evaluate the proposed negative relationship between both home range size and daily movement rate with habitat quality.
3) Evaluate an observed correlation between home range size and daily movement rate.
4) Compare home range size and overlap estimates of four contemporary home range models.

Answers to these questions can help researchers find metrics to measure moose-habitat relationships, understand space use patterns, determine the applicability of common home range models, and aid management of moose populations and habitat on the Kenai Peninsula and throughout Alaska.

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Chapter 2 Energetics and Space Use of Female Moose during Winter in Lowland and Mountain Landscapes: Is the Speed of the Slide Related to the Slope of the Hill?[1]

2.1 Abstract

I combined body condition with space use and habitat information to obtain insights into moose-habitat relationships on the Kenai Peninsula, Alaska, USA. I applied a repeated measures analysis to the estimated percentage of ingesta-free body fat (IFBF) of adult female moose during fall and spring to compare the energetic consequences of wintering in lowland and mountain landscapes. I found differing energetic consequences between the two landscape types. Mountain moose came into winter in better condition, but used fat at a faster rate resulting in similar IFBF levels for both landscape types in early spring. Mountain landscapes had higher snow depths and colder temperatures, which increase energetic costs and reduce forage availability. The different environmental conditions of the two landscapes likely explains the observed fat use differences. Using IFBF as an indicator of realized habitat quality, I also examined the proposed negative relationship between home range size and habitat quality. To minimize bias associated with investigating habitat quality, I applied high-resolution home range models to high-frequency location data. I did not find evidence to support the negative relationship between home range size and habitat quality, but

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did find evidence of a functional response of second order habitat selection within landscape types. These findings suggest that home range size alone is not a good metric of habitat quality for moose during winter. However, combining fitness measures, such as body condition, with space use and habitat information can provide sound insights into wildlife-habitat relationships.

2.2 Introduction

2.2.1 Habitat, Energetics, and Space Use

Habitat largely determines animal fitness and space use. Habitat is used here to mean all resources (e.g., forage and shelter) and environmental conditions (e.g., precipitation, snow depth, presence of predators) present (Gaillard et al. 2010). The synonymous terms habitat quality and habitat productivity are commonly used when referencing the influence of habitat on animal fitness and energetics. The terms describe the capability of habitat to provide the life history requirements of the animal. High quality habitat provide the variety of life history requirements, which increase fitness while maximizing energetic gains. Disparity in habitat quality is due to environmental conditions, intra- and interspecific interactions, and differences in the availability, quality, and juxtaposition of resources (Owen-Smith et al. 2010). In a given geographic region, habitat quality varies spatially (due to different habitat configurations) and temporally

(e.g., summer vs. winter). Examples of resources that can affect habitat quality include food abundance, food quality, patch size, distances between patches, spatial distribution of resources, cost of locomotion, cover from predators, human disturbance, thermal cover, and climate (Lyon 1987, Franklin et al. 2000, Thomas et al. 2001, Dussault et al. 2005a and b, Dussault et al. 2006, Herfindal et al. 2009).

Biologists use animal body condition or space use estimates to gain insights into habitat quality and wildlife-habitat relationships. Those estimates and resultant insights are often influential to wildlife management programs (Dussault et al. 2005b, Boertje et al. 2007, Boertje et al. 2009, Parker et al. 2009).

Animal body condition has been used as an indicator of habitat quality and population demographics (Franzmann and Schwartz 1985, Hobbs 1989, Schwartz and Renecker 1998, Stephenson et al. 1998, Parker et al. 2009, Cook et al. 2010). The animal indicator concept is used when body condition and/or fitness information are used to make inferences into habitat quality (Franzmann et al. 1995). This method of inference is based on the premise that body condition and reproductive output are the products of the quality and quantity of resources used by an animal. Body condition can be estimated indirectly by measuring reproductive output (e.g., Franzmann and Schwartz 1985) or directly by measuring body components (e.g., Stephenson et al 1998). Fat is a body component often used to estimate body condition. Female ungulates, including

moose (*Alces alces*), with high fat levels produce heavier calves, have more twins, give birth earlier in the spring, and have higher birth rates (Heard et al. 1997, Testa and Adams 1998, Keech et al. 1999, Keech et al. 2000, Parker et al. 2009). In addition, body mass and fat levels can influence calf survival (Cameron and Ver Hoef 1994, Keech et al. 2000). Fat measures have been used on a single demographic group during a single season to compare body condition (Cameron and Ver Hoef 1994).

The maximum depth of rump fat thickness (MAXFAT), measured via ultrasound, is a fat depot often used for ungulates (Cook et al. 2010). MAXFAT is an easily interpretable body condition estimate. In moose, it is linearly related to the percent of ingesta-free body fat (IFBF; Stephenson et al. 1998). MAXFAT estimates standardized across species, age, body size, sex, and time can provide insights into habitat quality. High IFBF values are indicative of high quality habitat encountered by an animal. Several researchers recommend MAXFAT estimates because they allow repeated *in vivo* measures of IFBF and a tool for the valuation of habitat quality encountered by animals (Stephenson et al. 1998, Stephenson et al. 2002, Parker et al. 2009, Cook et al. 2010).

Space use parameters have also been used as indicators of habitat quality (Allen et al. 1988, Winker et al. 1995, Reylea et al. 2000, Dussault et al. 2005b, Reid et al. 2007). Space use is used to denote all movement processes including home range, movement rate, migration, immigration, emigration and spatial resource/habitat selection. Home

range is used here to mean, "the extent of area with a defined probability of occurrence of an animal during a specified time period" (Kernohan et al. 2001: 126).

Researchers have investigated the determinants of home range size (HRS; Tufto et al. 1996, McLoughlin and Ferguson 2000, Börger et al. 2006, Herfindal et al. 2009, Schradin et al. 2010) since the formulation of the most recognized home range concept (Burt 1943). Home range size is the result of a complex interaction of factors (Relyea et al. 2000). McNab's bioenergetics-home range hypothesis (1963) deemed body size as an important determinant of HRS. Animals with larger body size, and associated higher metabolic requirements, have larger home ranges to meet their energetic needs. This hypothesis explains inter-specific variation across trophic levels very well (carnivore vs. omnivore vs. herbivore), but it is not as accurate explaining intra-specific variation. McNab suggested it was probable that factors other than animal bioenergetics also are important. As predicted, sixteen years later Harestad and Bunnell (1979) extended the bioenergetics-home range size hypothesis to include the habitat productivity-home range size extension. They state, "Indeed, there is no compelling reason to believe that metabolic rate should govern size of the home range or feeding territory independent of the distribution of the food resources" (Harestad and Bunnell 1979:398). This extension hypothesizes that habitat productivity and the distribution of resources also play an important role determining HRS. A proposed corollary of the habitat productivity-home range size extension that has implications on using space use as an

indicator of habitat quality is, "Within a specific trophic group and weight-class, habitats of greater productivity will generate smaller home ranges..." (Harestad and Bunnell 1979:394). The corollary postulates a negative relationship between habitat quality and HRS. As habitat quality increases HRS decreases and as habitat quality decreases HRS increases (Owen-Smith et al. 2010). This relationship assumes that habitat quality is higher within smaller estimated home ranges because a smaller area is capable of supporting the animal, while larger estimated home ranges are the result of poor quality habitat and a larger area needed to support the animal's life history requirements. The Harestad and Bunnell model is still an excellent conceptual model (Harestad and Bunnell 1979).

McLoughlin and Ferguson (2000) further amended the hypothesis by explaining that different factors act upon HRS at different scales (species, population, and individual levels). They hypothesize that food availability followed by distribution of resources, cover from predators, population density, and sex are most important at the individual level. They also state that males adjust their HRS to optimize breeding success, while females attempt to optimize food availability and cover. This makes females good candidates for examining the influence of habitat quality on space use. The current perception in the ecological community is, "The distribution of food and cover is probably most influential in affecting local movements within a home range" (McDonald et al. 2005:466).

The habitat productivity-home range size hypothesis has been supplemented to include daily movement rate (DMR) as a space use parameter related to habitat quality (Dussault et al. 2005b). Similar to HRS, DMR is a space use parameter presumed to have a negative relationship with habitat quality (Dussault et al. 2005b). HRS and DMR have been used singularly or in combination to make inferences into moose habitat quality (Dussault et al. 2005b and Herfindal et al. 2009). In general, it is now a commonly held belief that there is a negative relationship between both HRS and DMR with the quality of habitat encountered by the animal (Mitchell and Powell 2008).

From the habitat/resource selection perspective, the functional response of habitat selection hypothesizes that home ranges are constructed (second order habitat selection (Johnson 1980)) so that at least the minimum amount of limiting resources are encompassed within the home range (Mysterud and Ims 1998). In other words, HRS is a function of the juxtaposition of the limiting resources in the environment.

While space use has been documented as a correlate of habitat quality for several species (Tufto et al. 1996, Reylea et al. 2000, Anderson et al. 2005, Börger et al. 2006, Winker et al. 1995, Säid et al. 2009, Schradin et al. 2010), there is also empirical evidence of the functional response of habitat selection (Osko et al. 2004, Herfindal et al. 2009, Säid et al. 2009). Moose research indicates that HRS and DMR are dependent on habitat availability. Studies have found that moose select home ranges for forage,

cover, and the spatial distribution of those two resources (Dussault et al. 2005a, Dussault et al. 2006), there is a functional response of habitat selection at the home range scale (larger home ranges contain larger proportions of less preferred, and presumably less productive, habitats types; Osko et al. 2004, Dussault et al. 2005b, Herfindal et al. 2009), and population density has little effect on space use (Damuth 1981, Dussault et al. 2005b, Herfindal et al. 2009). High quality habitat for moose is dependent on the interspersion between forage and cover resources (Dussault et al. 2006). High quality moose habitat in the boreal forest is composed of shrub, deciduous, and mixed forest stands (i.e., forage patches) interspersed with mature coniferous forest (i.e., cover patches; Dussault et al. 2006).

While previous scientific inquiry has laid the foundations of wildlife-habitat relationships new technology and techniques produce more robust tools for the contemporary biologist. Traditionally, body condition estimates are not usually measured concurrent with space use and habitat information. It not unusual for researchers to use only space use parameters as indicators of habitat quality (Dussault et al. 2005b, Reid et al. 2007, Owen-Smith et al. 2010). This method of inference into habitat quality may be a less expensive alternative that can provide information on the spatial distribution of animals, but the inferences derived from this method may not be robust because neither fitness, body condition, or habitat characteristics are measured directly. This poses the question; do space use parameters truly translate to body condition

information and ultimately habitat quality information? Another method of inference into habitat quality is based upon measuring vegetative and/or physical characteristics of habitat (Garshelis 2000). This is mostly justified for moose because forage availability is the best predictor of forage consumption (Månsson et al. 2007). Two assumptions of using direct habitat measures to estimate habitat quality are that the habitat parameters related to fitness are identified and measured and that the animals know the distribution of all resources available to them and how to use those resources optimally. These appear to be very strong assumptions. It seems that body condition estimates combined with habitat information can provide more direct inferences into habitat quality (Garshelis 2000, Beyer et al. 2010) and elucidate their relationship with space use parameters. As stated earlier, it has been assumed that smaller home ranges are composed of higher quality habitat and by definition high quality habitat results in better body condition. If using body condition (e.g., IFBF) is an indicator of habitat quality, then according to the proposed negative relationship between HRS and habitat quality, IFBF is expected to be negatively correlated to HRS. As HRS decreases, it is expected that observed IFBF levels be at or more likely above the IFBF population average. However, from the perspective of the functional response of habitat selection, smaller HRS does not necessarily indicate better body condition and hence habitat quality. It does however, infer that animals with different HRS can have similar body condition because the ratio of available utilizable energy to the cost of habitation in the

home range is similar and the amount of limiting resources within each home range is similar.

Previous research may also have applied home range models that do not accurately reflect habitat use in landscapes with patchily distributed resources. This may have severe consequences when operating under the premise that HRS is negatively correlated to habitat quality. Studies assuming the negative relationship between HRS and habitat quality have assumed habitat quality to be poor in large home ranges and high in small home ranges. However, the assumed poor habitat quality may simply have been the result of positively biased HRS estimates in patchy landscapes. Mitchell and Powell (2008) showed that contiguous home range models, such as minimum convex polygons, can misrepresent the quality, composition, and size of home ranges. When assuming the negative relationship between HRS and habitat quality, contiguous home range models in patchy landscapes negatively bias habitat quality estimates because such models include areas that are not actually used by the animal (Mitchell and Powell 2008). This bias is proportional to the patchiness of resource-bearing habitats within the landscape (Mitchell and Powell 2008). Simple by their derivation, contiguous home range models include areas not actually used by the animal into the home range estimate. Contiguous home range models cannot accurately demarcate home range boundaries. This is because animals use the environment linearly, but linear attributes are lost in contiguous home range models.

These issues are a research concern for most ungulates, including species such as moose, that utilize patchy, disturbed, and edge habitats (Peek 1998). Minimum convex polygons and measured habitat characteristics have been used to document the negative relationship of HRS and habitat quality in moose occupying patchy landscapes during winter and summer (Dussault et al. 2005b, Herfindal et al. 2009). This empirical evidence of the negative relationship may have actually been documenting study design artifacts due to the patchy landscapes moose inhabit, the use contiguous home range models, and habitat quality measures based on direct habitat measures rather than using the animal indicator concept (Franzmann et al. 1995). Therefore, it would be beneficial to reevaluate the negative relationship between HRS and habitat quality using body condition information combined with high-frequency location data and a home range model capable of producing fine-scale use estimates.

2.2.2 Winter Energetics and Space Use

Ungulates inhabiting environments of variable nutrition are able to anticipate periods of catabolism (winter or dry season) and anabolism (summer or wet season). Wildlife, especially large mobile species living in areas with elevation or longitudinal clines, move to certain areas during certain times to find optimal habitat conditions (maximize resource acquisition, reduce competition, evade predators, reproduce, and find favored thermal cover; Hundertmark 1998, Owen–Smith et al. 2010). During winter, moose

either migrate or remain sedentary (Hundertmark 1998). Within a single population individuals use both wintering strategies. Moose occurring in lowland and mountain landscape have been observed as both migratory and sedentary (Hundertmark 1998).

Historically, winter habitat is usually considered critical for subarctic and arctic ungulates because they experience a negative energy balance and mortality related to poor nutrition during this time (Thompson and Stewart 1998). During winter, environmental conditions may increase the cost of or inhibit movements and reduce forage quality and availability. Snow makes movement an expensive activity and high snow depths cover forage reducing its availability (Renecker and Schwartz 1998). Severe exposure and cold also increase metabolic costs (Schwartz and Renecker 1998). Because of the above habitat conditions, moose go into negative energy balance and rely heavily on stored energy reserves, primarily fat and protein (Parker et al. 2009). Their large body size enables the ability to store large reserves for use throughout the long winters (Mysterud et al. 2001). Ultimately, the overwintering strategy of moose is to decrease forage intake in order to decrease body mass and reduce activity in order to decrease energy use (Schwartz and Renecker 1998, Parker et al. 2009). The combination of factors suggest that a sedentary life-style in patches of cover would be optimal during winter. However, because forage does not regenerate during winter animals are forced to expand their home ranges to access new foraging areas (Owen-Smith et al. 2010, Chapter 3).

To describe the energy balance of ungulates during winter, Mautz (1978) used the analogy of sledding down a winter hillside on runs composed of various shrub densities. If deer reach the bottom of the hill they die, but shrubs (i.e., food) can slow their rate of descent and stop the deer from reaching the bottom of the hill. This analogy elucidates the fact that the magnitude and rate of consumption of stored body reserves are strongly related to the energy reserves stored prior to winter and the forage availability and quality encountered during winter. It is becoming increasingly recognized that late fall body fat levels and nutrition during the periods of vegetative production are also important determinants of the annual bioenergetics of northern ungulates (Parker et al. 2009). Moose, in particular, must build up large fat reserves by consuming productive green plant growth during the growing season to compensate for less abundant and low quality forage during winter. Therefore, if moose are able to accumulate large stored body reserves they can endure extended sled runs. Large stored body reserves coupled with use of prime winter forage areas may ameliorate the amplitude of the low point in the annual cycle of the energy balance.

2.2.3 Objectives

Individuals of a moose population inhabiting the north-central region of the Kenai Peninsula, Alaska, USA winter in both lowland and mountain landscapes. Local wildlife managers observed differences in the habitat composition between the two landscape

types and speculated that the observed disparity in habitat composition may translate into habitat quality differences between the two landscapes during winter. Managers were interested in examining the advantages and disadvantages of using each landscape type. The objective of this research was to determine how HRS, DMR, reproductive costs, and landscape type affect body condition during winter. I examined the energetic consequences of moose wintering in lowland and mountain landscapes. Specifically, I examined if IFBF and the magnitude and rate of fat mobilization are related to the landscape type used. I also evaluated the proposed negative relationship between habitat quality with HRS and DMR using IFBF as an indicator of habitat quality (do smaller HRS and DMR translate into better body condition?). I used high-frequency global positioning system (GPS) data and a home range model that allow very fine resolution of use estimates. I hypothesized that the landscape type used during winter will result in different IFBF and fat mobilization rates. I speculated that in fall, mountain moose will have greater IFBF than lowland moose because of access to better forage abundance and quality in the mountains during summer due prolonged access to succulent plant growth. I also speculated mountain cows will use fat reserves at a higher rate due to exposure to more severe winter conditions (e.g., deeper snow depths, less available forage, and colder temperatures). I was uncertain as to which landscape would result in higher end-of-winter IFBF estimates. I also hypothesized that space use is negatively correlated with body condition and hence habitat quality. Answers to these questions will help provide an understanding of moose adaptability

and baseline habitat relationship information in the face of changing climate conditions on the Kenai Peninsula (Klein et al. 2005).

2.3 Methods

2.3.1 Study Area

This study was conducted on the Kenai Peninsula in south-central Alaska, USA (Figure 2.1). The Kenai Peninsula is nearly 26,000 km^2 and approximately 35 km south of the largest urban area in Alaska (the Anchorage Bowl and Matanuska-Susitna metropolitan areas). The eastern two-thirds of the peninsula is primarily composed of mountains, while the western one-third is made up of lowlands. The study area is located in the north-central region of the peninsula. It is bisected east and west by lowland and mountain landscape types while the Sterling Highway runs through the southern region of the study area. The study area boundary is delineated by a minimum convex polygon, constructed from the locations of all collared cows and a 1416 m external buffer. The external buffer was calculated as half the mean maximum distance moved between successive GPS locations of all cows (Figure 2.1).

I classified lowland and mountain landscape types by ecoregions created by Nowacki et al. (2001). Ecoregions are defined by climate, topography, vegetation, lithology, and surficial deposits. I refer to the Cook Inlet Basin ecoregion as the lowland landscape and

the Chugach-St. Elias Mountains ecoregion as the mountain landscape. Lowland landscapes are characterized by elevations near sea level and low variability in elevation gradient. The majority of lowlands have poorly drained soils that support black spruce (*Picea mariana*) forests and woodlands. Sitka spruce (*Picea sitchensis*), white spruce (*Picea glauca*), aspen (*Populus tremuloides)* , birch (*Betula spp.*) and tall shrubs are present on the well drained soils. Birch-spruce forests of the lowlands are in various successional stages due to natural and manmade fires, insect infestations, and mechanical treatments implemented specifically to increase available forage for moose. The boreal lowlands are considered a transitory landscape, shifting between successional stages. The lowland landscape is more dynamic than the mountains, as fire, climate change, insect infestation, and anthropogenic activities alter biotic communities (Klein et al. 2005, Boucher and Mead 2006). Study animals of the lowlands occurred on the Kenai National Wildlife Refuge and some private lands. The mountain landscape is characterized by high variability in elevation gradient. Mountains are primarily composed of climax habitat. High elevations are composed of alpine habitats such as low shrubs, sedges (*Carex spp.*), and grasses. At lower elevations, habitats such as willow-shrub (*Salix spp.*) and alder-shrub (*Alnus spp.*) complexes, headwater riparian, and mixed-conifer forest are prevalent. Study animals in the mountains occurred primarily within Chugach National Forest and private lands along the Kenai River. Major winter browse species in the study area include aspen, birch, and willow. Detailed vegetation maps of the area can be found at Kenai Peninsula Borough, Spruce Bark

Beetle Mitigation Program website (http://www.borough.kenai.ak.us/sbb). Other large mammals in the study area include black bear (*Ursus americanus*), brown bear (*Ursus arctos*), caribou (*Rangifer tarandus*), coyote (*Canis latrans*), Dall sheep (*Ovis dalli*), red fox (*Vulpes vulpes*), wolf (*Canus lupus*), and wolverine (*Gulo gulo*).

Environmental conditions such as snowfall, snow depth, wind, slope, and temperature vary between the two landscapes types by typical elevation clines. Snow is generally present in the mountains from September through May and in the lowlands from October through April (Bangs and Bailey 1982). Weather data collected at the Kenai Moose Research Center, SNOTEL station 966, at an elevtion of 91 m, for temperature and precipitation during the study period were: mean daily low temperature was -15.9°C, mean daily high temperature was -4.6°C, mean daily snow depth was 35.8 cm, 12.7 cm of snow the first day of the study, and 48.3 cm of snow the last day of the study (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=966&state=ak). These data are representative of the lowlands. Weather data collected at Summit Lake NRCS SNOTEL station 955, at an elevation of 426, were: mean low daily temperature was -16.85°C, mean high daily temperature was -6.8°C, mean daily snow depth was 75.1 cm, 15.2 cm of snow the first day of the study, 99.1 cm of snow the last day of the study (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=955&state=ak). These data are representative of the mountain landscape during the study period (Table 2.1).

2.3.2 Captures

Captures for this project ran concurrent with captures for other related research projects. Therefore, cows were captured opportunistically, but with an effort to spread captures representatively throughout the study area. Cows were initially captured during one week at the end of October-beginning of November 2006. I refer to this capture period as fall. Moose were in post-rut, mixed-sex aggregations during this period. Cows were subsequently recaptured during one week at the end of March-beginning of April 2007. I refer to this capture period as spring. To avoid capture artifacts and standardize the monitoring period, all location data were censored 5 days subsequent to the last moose captured in fall and after the first capture in spring. This resulted in a monitoring period of November 12, 2006 to March 31, 2007. Collared cows were assigned to lowland and mountain groups by determining the majority of their recorded locations in each landscape type over the course of the winter.

To minimize capture costs, moose were initially spotted from a Piper PA-18 Super Cub. The Super Cub crew relayed locations of moose available for capture to the capture crew on standby in a Robinson R-44 helicopter. Moose were pursued and captured from a helicopter using projectile chemical immobilization. Collared cows were also recaptured from the ground during spring via chemical immobilization. Cows were immobilized with a mixture of 3.5 to 5.0 mg carfentanil citrate (Wildnil®; Wildlife

Pharmaceuticals, Fort Collins, CO) and 40 to 100 mg xylazine hydrochloride (Anased®; Lloyd Laboratories, Shenandoah, IA) in a 2cc Cap-Chur dart™ with 1.25" barbed needle shot from a Palmer Cap-Chur™ rifle into hind and front quarter major muscle masses. Drug dosages were dependent on the specific situation and condition of the animal. Antagonist consisted of 100 mg naltrexone hydrochloride (Trexonil®; Wildlife Pharmaceuticals) per 1 mg of carfentanil citrate and 0.5 mg tolazaline hydrochloride (Tolazine®; Lloyd Laboraties) per pound of estimated body weight. Antagonist was administered 25% intravenous and 75% intramuscular with a hand syringe. During anesthesia, rectal body temperature and respiration rate were continuously monitored. All immobilization times were less than 45 minutes. After the antagonist was administered moose were observed from a safe distance until the animal was able to stand and retain motor function.

During fall captures, Telonics model TGW 3600 GPS/VHF collars (Telonics, Mesa, Arizona, USA) were placed on cows. Three cows from the mountain group were also fit with Televilt collars (Televilt, Lindesberg, Sweden). Two ear tags were placed in each animal for visual identification. MAXFAT was estimated with a b-mode Bantam Ultrasound Scanner with a 5.0MHz Linear Transducer (E.I. Medical Imaging, Loveland, Colorado, USA) following the procedures of Stephenson et al. (1998) and Gustine et al. (2006). A small patch of hair was removed from the skin over the measured fat depot. The skin was lubricated with canola oil or ultrasound gel and MAXFAT was measured to

the nearest mm. MAXFAT measures were primarily taken by me and another researcher. For a portion of the cows, measurements were taken concurrently by both researchers to ensure consistency in MAXFAT estimates. Other variables recorded during capture include estimated age and presence of other moose. During spring captures the same procedures were applied with that exception that collars were removed. All field and capture methods were approved by Alaska Department of Fish and Game, Animal Care and Use Committee, Assurance No. 06-03.

2.3.3 Space Use Parameters

GPS collars were programmed by personnel from separate state and federal agencies with different objectives. This resulted in location intervals of approximately 15, 30, 70, or 120 minutes. All location intervals were truncated to the same even-numbered two hour intervals (except for two cows in the lowland group and two cows in the mountain group that were truncated to two hour and 20 minute intervals due to programming). Telonics collar location data were screened by removing locations with positional dilution of precision (PDOP) > ten for three-dimensional locations and PDOP > six for two-dimensional locations. Locations were mapped in ArcGIS (Environmental Systems Resource Institutem, 2009, ArcMap 9.2, ESRI, Redlands, California) and any unrealistic locations (e.g., locations in the ocean) were also removed. This screening strategy is a combination of the recommendations of O'Neil et al. (2005) and Lewis et al. (2007).

Televilt collar data were screened by Western Ecosystems Technology (WEST), Inc. (Cheyenne, Wyoming, USA). All three-dimensional locations were retained that had PDOP values < ten. Unrealistic mapped locations were also removed after WEST screening.

Daily movement rate was calculated as the mean three-dimensional distance moved over one hour intervals. Mean elevation per landscape group was calculated as the mean of the observed GPS elevation measurements within individuals and then averaging the individual cow means within landscape groups after screening locations. This allowed each individual to contribute equal weight (individuals with more locations would not influence the mean more than individuals with fewer locations and vice versa).

HRS was estimated using Brownian bridge movement models (Horne et al. 2007). Brownian bridge movement model probability density grids were constructed using the software Animal Space Use 1.3 (Horne and Garton 2009). Grid extents were estimated as the greatest north and east location coordinates plus 700 m and the minimum south and west location coordinates minus 700 m. This ensured full coverage of the estimated utilization distribution. Maximum time intervals between locations used to estimate utilization distributions ranged from 240 to 1121 minutes (mean = 472 minutes). Grid cell size was set to 25 m for all individuals. Grids were imported into ArcGIS as point

features, converted to rasters, the rasters were then reclassified by grouping all valued cells into one class, then reclassified rasters were converted to polygons using the simplified option.

2.3.4 Analysis

MAXFAT estimates were converted to IFBF values from regression equations developed for adult cow moose by Stephenson et al. (1998). The conversion equation of MAXFAT to IFBF is

$$IFBF = 5.61 + 2.05 * MAXFAT.$$

I used a repeated measures (i.e., longitudinal) analysis (Pinheiro and Bates 2000, Crawley 2007, Zuur et al. 2009, Bates 2010) to determine how landscape type used during winter (lowland vs. mountain), season (fall vs. winter), and HRS influence estimated IFBF. Model selection was performed using Akiake's second order information criterion to determine parameter estimates and the importance of variables (AICc; Burnham and Anderson 2002). Over-parameterization of the models was a concern due to the small sample size relative to the number of variables of interest. Kutner et al. (2005), suggest six to ten cases for every variable. I eliminated one variable of interest prior to constructing models. The two space use parameters, HRS and DMR, were highly correlated, $r = 0.87$ (Figure 2.3 and 2.4). Due to the degree of correlation,

concerns of multicollinearity, and my primary interest in HRS related to energetics and habitat quality, I excluded DMR from model selection. I also excluded the variable presence of calf from the all subsets model selection because only three out of the 40 (7.5%) cows were observed with calves. Variables included in the a priori all subsets analysis were HRS, landscape type (lowland vs. mountain), and season (fall vs. spring). I followed a modeling protocol developed by Zuur et al. (2009) that uses maximum likelihood and restricted maximum likelihood estimation to construct linear, generalized least squares (gls), and linear mixed effects (lme) models to model different variance-covariance structures and make model selection inference.

The first stage of the protocol was determining the random error structure of the models. The random error structure was determined through model selection of linear, gls, and lme maximal models (all fixed effects included) using restricted maximum likelihood estimation. First the variance structure of random error component was determined, then the correlation structure was determined. For lme models, random effects were determined prior to variance and correlation structure. The random effects covariate was specified as season, which was grouped by individual. Random effects were also modeled as random intercepts. Random error variance structures specified in lme models were fixed identity based upon landscape, season, or both or power of the covariate based on season or fitted values. Random error variance in gls models was specified as fixed variance structure based on HRS, power of the covariate

variance structure for season and fitted values, fixed identity based on season, landscape, or both factor levels, exponential variance structure, or constant plus power of the covariate variances. Residual correlation structure in lme and gls models was specified as null or compound symmetric dependent on the individual. For my data, with only two repeated measures, compound symmetric correlation is equivalent to symmetric and auto-regressive first order correlation models. Finally, for comparison, a linear model without random effects or an adjusted variance-covariance structure was constructed. I also determined the correlation of the random effects, intercept and slope, using the maximal lme model and model selection.

After the random error structure was determined, the second stage of the protocol is resolving the fixed effects structure of the models. Fixed effects were determined using model selection via maximum likelihood estimation. During model selection, all subsets of fixed effects were considered. For the final stage of the protocol, the parameter estimates of models were recalculated via restricted maximum likelihood estimation. The software R (R Development Core Team 2010) and package nlme (Pinheiro et al. 2009) were used to construct linear, gls, and lme models. The lmer function, from the R lme4 package (Bates and Maechler 2010), was used to test for correlation of the random effects fall IFBF and IFBF use (Bates 2010). All model selection calculations were completed with the R package, AICcmodavg (Mazerolle 2009).

2.4 Results

Sample size was 29 lowland and 11 mountain cows (Table 2.2, Figure 2.2). For the lowland group, I obtained 15 cows with both fall and spring MAXFAT measures, 13 cows with only fall measures, and one cow with only spring MAXFAT measured. Of the cows captured in the lowlands, only one spent any time in the mountains and this cow had 98% of its locations in the lowlands. In total, 14 cows were captured in the mountains, but three are included in the lowland group because 91, 89, and 62% of their locations occurred in the lowlands. I obtained data from five mountain cows with both fall and spring MAXFAT measures, one cow with only fall MAXFAT measures, and five cows with only spring MAXFAT measures. Six of the 14 cows captured in the mountains spent some time in the lowland landscape during late winter. Of those six cows, the percentage of observed locations in the lowlands ranged from 20% to 91% of all locations (as mentioned earlier three of these cows were included in the lowland group). Most of the cows initially captured from the mountain group were in, or near Juneau Creek drainage, Chugach National Forest, while most lowland cows were initially captured in, or near Skilak Lake Management Area, Kenai National Wildlife Refuge. Mean observed elevation of lowland and mountain groups were 138 m (sd = 49 m) and 427 m (sd = 96 m), respectively.

Median HRS estimates of lowland and mountain groups was 2601.37 and 2047.92 ha respectively (Figure 2.5) and mean HRS estimates for lowland and mountain groups was 3064.49 (sd = 1810.32) and 2433.43 (sd = 1282.66) ha respectively. Median DMR estimates of lowland and mountain groups was 48.29 and 38.43 m/hr respectively (Figure 2.6) and mean DMR estimates for lowland and mountain groups was 49.30 (sd = 11.98) and 40.55 (sd = 8.58) m/hr respectively.

Prior to screening the Telonics location data, 0.997 (sd = 0.0028) of all attempted fixes were successful for the lowland group and 0.991 (sd = 0.0061) of all attempted fixes were successful for the mountain group. Three-dimensional fix-rate of all attempted fixes by Telonics collars for lowland and mountain groups were 0.88 (sd = 0.037) and 0.79 (sd = 0.039), respectively.

2.4.1 Random effects

The top random effects models were an lme model with random effects for the intercept and slope and a gls model with correlated structure within individual measurements and separate variances for fall and spring seasons (Table 2.3). Although the top lme had a slightly lower AICc (ΔAICc = 0.59), the fit of the model was poor, residual analysis indicated problems, and there were large confidence intervals on the random effects. Because the gls model fit the data, had desirable residuals, required no

transformations (which is an advantage because transformations can result of loss of interpretability), provided sensible estimates, was simpler than the lme model, and was very close to the lme model AICc value, I used the gls model to determine the fixed effects and for model inference. The next best model is 1.93 AICc units larger than the top gls model (Table 2.3). The traditional linear model is over 26 AICc units larger than the top gls model (Table 2.3).

2.4.2 Fixed effects

Model selection of the top gls model structure to determine fixed effects considered 19 models of all variable subsets (Table 2.4). The top model includes landscape, season, and their interaction. This model has 55% of the AICc weight. HRS was not a variable in the top model. According to the 2nd ranked model, with a ΔAICc of 2.64, HRS was a main effect that has a negative additive effect on IFBF estimates. However, in this case HRS is what is referred to as a "pretending variable" (Anderson 2008). The log likelihood is not improved by the inclusion of the variable, the ΔAICc increases by about two units (Table 2.4), and the coefficient confidence interval overlaps zero. Therefore, the second model was ranked high in spite of the uninformative variable HRS.

According to the top model, IFBF values for lowland fall was 13.21% (se = 0.60), 17.71% (se = 1.20) for mountain fall, 7.48% (se = 0.23) for lowland spring, and 7.69% (se = 0.31)

for mountain spring (Table 2.5). Fall IFBF 95% confidence intervals did not overlap, but spring values did (Table 2.5). Standard deviation for fall IFBF estimates was 3.21 (95% CI 2.35-4.37) and 1.00 (95% CI 0.76-1.32) for the spring. Correlation between fall and spring IFBF estimates within individuals was 0.61 (95% CI 0.29-0.81).

Model selection of the lmer models indicated a very high negative correlation (-0.99) between the random intercept, fall IFBF, and the random slope, IFBF rate of change, (ΔAICc = 2).

2.5 Discussion

2.5.1 Energetic Consequences of Wintering in Lowland and Mountain Landscapes

Based upon model selection, validation, and simplicity, I chose to use the top gls model to model the random error structure. Fixed effects model selection indicated that IFBF was dependent on season (which is not a surprise for ungulates) and landscape type, but not HRS (Table 2.4). Mountain moose came into winter in better condition, but mobilized fat at a higher rate than lowland moose resulting in similar IFBF estimates for both groups during spring recaptures (Figure 2.7). The rate and magnitude of consuming stored body reserves, such as fat, is strongly related to the ratio of the available utilizable energy in the environment to the cost of habitation in the

environment. The output from the top model suggests that a strategy to spend summer and fall in the mountains and winter in the lowlands may result in highest IFBF values (Figure 2.7, Table 2.5). As mentioned earlier, Mautz's (1978) sledding analogy is dependent on shrub densities. This study suggests the speed of the slide is also dependent on the height and steepness of the hill. Because mountain cows had a higher IFBF and rate of fat use, they had faster and longer slides than the lowland cows. From this study I cannot determine if available utilizable energy is greater in one landscape or another, but I can state that the ratio of available utilizable energy to cost of habitation is lower in mountain than lowland landscapes during winter. Because mountain cows came into winter in better condition than lowland cows, but used fat at a higher rate during winter, I am led to conclude that lowland landscapes were less of an energetic drain and higher quality habitat during the study. Initially, I speculated that the habitat quality of mountain hillsides might be comparable to the lowland forests during winter due to the large willow stands present in the mountain landscape in spite of increased weather severity. However, winter conditions in the mountains may have negated the willow forage effect. Consequently, steep hills with many shrubs may still result in high sledding speeds.

Difference in forage availability and weather conditions are almost certainly the primary reasons for the observed differences in IFBF values and the rate of fat use between the two landscape types. Observed IFBF values reflect habitat and weather conditions

because this study controlled sex, age, and incidentally costs of reproduction (because almost all cows had no calves). Fall body fat levels are the result of access to nutrition during vegetative greenness and costs associated with rearing offspring (Parker et al. 2009). Because mountain cows had higher fall IFBF, they had access to better habitat during the summer and fall or did not experience the energetic burdens of gestation and lactation as long as lowland cows did (Figure 2.2).

Throughout the study period mountain landscapes had greater snow depths and colder temperatures than lowland landscapes (Table 2.1). The more severe environmental conditions in the mountains increased movement and metabolic costs, while at the same time decreased forage availability resulting in the higher rate of fat use observed in mountain cows. Mountain landscapes also have more variability in elevation, which can increase energy expenditure due to increased locomotion costs of moving uphill. However, even if forage availability and quality were similar for lowland and mountain landscapes the higher costs associated with movement and thermoregulation may explain the higher rate of fat use observed in mountain cows. Alternatively, the reduced forage availability of the mountains, alone, may explain the observed differences in fat use. It is also possible that the spatial distributions of forage and cover differs between the two landscapes and the spatial distribution of forage and cover is important to moose at the landscape and home range scale (Dussault et al. 2005a, Dussault et al. 2006). Regardless, the empirical results of this study lead to the conclusion that lowland

landscapes are less of an energetic drain during winter or i.e., lowland landscapes provided better habitat quality during winter during this study year.

This raises the question; why do moose choose to winter in the supposed inferior mountain landscapes? Moose habitat selection has been seen as a trade-off between forage and cover resources (Dussault et al. 2005a, Dussault et al. 2006). Forages patches contain nutrition needed for survival, but usually increase risk of predation and exposure to severe weather, while cover patches provide protection for environmental conditions such as predation and severe weather, but usually do not provide abundant forage resources (Dussault et al. 2005a, Dussault et al. 2006). Landscape selection is probably related to the most important limiting factor, which for moose has been postulated as predation risk (Dussault et al. 2005a). Moose may choose to winter in poor quality mountain landscapes to minimize predation risk, which may be the primary limiting factor. Wolves are the major predator of moose during winter. Moose may avoid wolves by using areas that wolves cannot because of deep snow depths (Peek 1998, Dussault et al. 2005a). However, wolf kills were observed in both landscapes during the study. The trade-off for reduced predation risk may be decreased forage availability and ultimately result in a greater energy deficit (Dussault et al. 2005a). It is also very probable that habitat quality is not static and that mountain landscapes may provide higher quality habitat than lowlands during some winters and vice versa. Studies have shown that the areas moose use during winter are dependent on winter

severity (Stephenson et al. 2006). Perhaps during winters of low snow accumulation the forage availability of the mountain landscape is not compromised and the mountains can provide more productive wintering areas than the lowlands. During the winter following this study, mountain moose had higher spring IFBF estimates than the lowland and mountain moose of this study (Kraft unpublished data). The simplest explanation for moose wintering in inferior quality habitat is that population growth promotes population range expansion to areas of lesser habitat quality and the fact that there is temporal variation in habitat composition and quality.

Mountain moose in this study can be considered elevational migrants during winter. They were initially captured in post-rutting aggregations at the highest elevations they were observed. As winter progressed, increasing snow depths and decreasing forage availability forced this group to move to lower elevations though most still remained in the mountain landscape. Is this movement strategy the byproduct of following succulent forage up elevational clines during the summer and fall? It may be that mountain cows compensate for poor quality habitat during winter by following highly productive emergent new growth up elevations as summer progresses to acquire very high quality forage from phenologically young plants. An alternative explanation is that mountain moose move to high elevation areas to facilitate harem breeding. These hypotheses raise the question; why did these moose evolve to move to higher

elevations during the fall? To facilitate reproduction or follow vegetation green up or both?

In addition to landscape type used during winter, the results also suggest that fall body condition affects winter energetics. The rate and magnitude of fat use during winter is positively related to the amount of accumulated fat stores prior to winter. Model selection of lmer models indicated that the random effects fall MAXFAT and MAXFAT rate of change through winter were highly negatively correlated (-0.99). This translates to high fall fat values resulting in high rates of fat use through winter. Moose in good body condition may have the luxury of using fat reserves less conservatively than individuals that come into winter in poor condition. This raises another question; are moose in good condition mobilizing more fat as a response to the environment or simply because they can without incurring any fitness costs? It is more probable that it is an environmental response. Surely, any animal would try to stay most fit (i.e., better body condition) during times of food shortages. This reinforces the idea that summer nutrition is also very important to winter energetics. Parker et al. (2009) state that nutrition is the most important determinant of population sustainability and that in northern environments, such as those that moose inhabit, management should be directed at providing the most nutrient gain between spring and fall for both sexes.

In Figure 2.7, it appears there are two natural groupings of fall IFBF values within the lowland group which are separated at around the IFBF values of 13.5%. I speculate that part of the observed disparity in fall IFBF values within the lowland group (Figure 2.7) is due to gestation and lactation costs. I speculate that the high IFBF individuals in the lowland group are the result of not incurring the energetic costs gestation and lactation for as a long a time as the low IFBF value group.

From a very coarse perspective this research may be considered a study into the effects of population resource selection on population fitness. During winter, individuals select either lowland or mountain landscapes, which results in different energetic consequences. Selection at this scale is predominantly on a generational scale (Gaillard et al. 2010). Selection in this case may be a combination of behavioral choices, ranging behaviors learned from the dam (Ballard et al. 1991), and the fact that being born into one of the landscape types will dictate which landscape is selected for winter range.

2.5.2 Examining the Negative Relationship between HRS and IFBF and the Functional Response of Habitat Selection

This study is also an evaluation of the proposed negative relationship between HRS and habitat quality. As stated earlier, this relationship is a corollary of the home range size hypothesis. This study of space use related to habitat quality is unique in that I applied

the animal indicator concept and used body condition as an indicator of habitat quality (Franzmann et al. 1995) as opposed to measuring habitat characteristics directly. Using body condition as an indicator of habitat quality can be viewed as measuring the realized habitat quality, whereas, using habitat characteristics to indentify habitat quality can be viewed as estimating the potential habitat quality.

Using body condition as an indicator of habitat quality, I did not find evidence of the negative relationship between space use and habitat quality. I believe the negative relationship between HRS and habitat quality may not be widely applicable to moose during winter. If the negative relationship between HRS and habitat quality was present, you would expect individuals with small HRS to have IFBF values of at least the level of the population average and individuals with larger HRS to have IFBF values below the population average (no evidence of this in Figures 2.3 and 2.4). You would also expect lowland moose to have smaller HRS than mountain moose on average because lowland moose used less fat during winter. However, small and large IFBF values are present throughout the observed range of HRS in both landscapes (Figure 2.3 and 2.4), the median HRS was similar for both landscapes types, and the right tail of the lowland type was skewed towards larger HRS estimates (Figure 2.5).

I found evidence of the functional response of habitat selection at the second order in the study system to a certain extent. Within landscapes, HRS was not an important

determinant of body condition. Cows were able to adjust HRS to encompass resources and maintain similar body condition. However, between landscapes the functional response of habitat selection is not as evident. Median and mean HRS in lowland and mountain cows was similar (Figure 2.5), but mountain moose used fat at a higher rate (Figures 2.6). Consequently, cows in the mountain landscape were not able to adjust HRS during winter to slow the rate of fat use to that of lowland cows. As stated earlier, an alternative explanation is that mountain cows were able to use fat at a higher rate simply because they had the luxury of mobilizing excess stored fat.

Variation in cost of movement and available resources between landscape types may also explain why the functional response of habitat was not evident across landscapes. In this study system, the increased costs of movement in the mountains probably could not be compensated for by the available utilizable energy. Because of more extreme winter conditions, mountain cows may never achieve the ratio of available utilizable energy to cost of habitation that lowlands offer by expanding their home ranges. Another reason may be that the same resources are not available in both landscapes, e.g., travel corridors in the lowlands, which mountain cows cannot compensate for if this resource is missing.

Moose space use during winter may be determined more by minimizing energy expenditure and relying on stored body reserves during winter, which occurs mainly

through reducing body mass and adjusting movements to habitat conditions, to the extent that efforts are not made to maximize energetic intake. During periods of less productive resources, animals often limit movement and energy expenditure (Schradin et al. 2010). As mentioned earlier, increasing snow depths and extreme temperatures increase movement and metabolic costs. Moose limit movement during severe weather (Hundertmark 1998) and use body postures in an attempt to remain in their thermoneutral zone (Schwartz and Renecker 1998). In fact, in circumstances of very limited resources, HRS may be positively correlated to habitat quality, "...if the costs of increasing home range size to search for food is not compensated by energy gains, then home range size may decrease with decreases in food availability" (McLoughlin and Ferguson 2000, see also Owen-Smith et al. 2010). Cows in both landscapes may rely on fat reserves and reduce energy expenditure to the extent that habitat quality is not a constant determinant of space use during all or part of winter. An alternative explanation for the lack of correlation is simply the possibility that there was not enough variation in habitat quality to induce a HRS effect. It is also possible that the home range estimates were still too contiguous to measure habitat quality without bias, although this study was designed specifically to control for such variables. Another possible explanation is the functional response of habitat selection at the home range scale as discussed above.

I accounted for bioenergetic differences related to the home range size hypothesis. While I did not measure energetic requirements of cows such as body size, pregnancy status, reproductive costs during summer, and cost of locomotion, I did control for bioenergetic influences by observing a single sex and age class and individuals with similar reproductive costs during winter (no calves at heel). When shaping intraspecific HRS, variation in body size may be less important than other factors such as habitat quality and reproductive activities (Relyea et al. 2000). I did not expect population density to influence IFBF or space use estimates between landscapes as the density of moose in the two landscapes was similar (personal communication, Thomas McDonough, Alaska Department of Fish & Game). Additionally, due to their large body size (Damuth 1981) and lack of empirical evidence (Herfindal et al. 2009), it is not believed that population density has a strong effect on HRS in large mammals such as moose. Because of the above controls, the observed differences in home range size are likely due to behavioral and habitat characteristics. I am uncertain as to which habitat characteristics, but food, cover, and weather are historically most important (McDonald et al. 2005). Therefore, based upon my findings, I argue that the home range size hypothesis is most useful at predicting the minimum area required to sustain an animal, but other factors such as breeding, reproduction, predation, and animal interactions are likely to increase the area actually used. The minimum area argument is supported by the fact the animals do not know all of the resources available to them in their environment or how to use them most optimally. Therefore, memory, exploration, and

chance are also important determinants of HRS. While previous research has documented the negative relationship between HRS and potential habitat quality (Dussault et al. 2005b, Herfindal et al. 2009), the relationship may be different for realized habitat quality. As stated earlier, previous research conclusions may also have been biased due to the use of contiguous home range models (e.g., minimum convex polygons). Ultimately, my findings do not support a relationship between body condition and HRS during winter. Therefore, HRS alone should not be used an indicator of habitat quality of cow moose during winter.

2.5.3 Benefits of Analytical Approach Used

Because I tested all subsets to determine the random and fixed effects, this analysis can be considered exploratory. However, the analytical approach used allows great flexibility and robust inference. This approach utilizes random effects and allows specification of the variance-covariance structure to account for within group correlation structure and heterogeneity of variance. Both gls and lme models are capable of modeling nested structure in the random component (Zuur et al. 2009:71). The gls models are essentially weighted linear regressions, while the random effects of lme models are the deviations from the fixed effects intercept and slope of each individual experimental unit (Bates 2010). The mixed-effects repeated-measures

analysis works well with missing data, which was crucial as there were not repeated IFBF measures on all study animals (Table 2.2, Figure 2.2).

Traditionally, ecological analyses do not model correlation or heterogeneity of the random error component, but this may be to the detriment of discovery. Zuur et al. (2009:72) discussing heterogeneity state,

> The easiest solution is a data transformation, but I try to avoid this for as long as possible. In our view, heterogeneity is interesting ecological information that you should not throw away, just because it is statistically inconvenient. With a 'little' bit of extra mathematical effort, heterogeneity can be incorporated into the model and can provide extra biological information.

Without such an analytical framework my insights would not have been as broad or robust. I was able to account for correlation between repeated IFBF estimates within the same individual and different variance structures for fall and spring IFBF estimates. This added biological realism and improved model fit drastically over the traditional linear model. Both gls and lme models had much smaller AICc values than traditional linear models (Table 2.3). Modeling serial autocorrelation between fall and spring IFBF estimates within the same individual is justified because it is intuitive that repeated IFBF estimates on the same individual are not independent and are more related than measurements taken on different individuals. Because data exploration indicated different variances for fall and spring IFBF estimates, I was also able to model separate

variance structures for fall and spring IFBF estimates. Different variances for fall and spring IFBF estimates are also biologically reasonable. It is likely there is greater variability in energetic levels during fall. High energy costs occur in late winter through summer for female ungulates (Schwartz and Renecker 1998, Parker et al. 2009). Cows endure gestation and lactation costs for different amounts of time due to differential survival of fetuses and neonates. Quality of available habitat also differs vastly during summer. Therefore, it is expected that there would be more variation in fall IFBF estimates. During winter, similar quality of forage resources, a negative energy balance, and mobilization of stored body reserves force cows to similar IFBF levels in spring.

2.5.4 Post-hoc analyses

After completing the formal analyses several questions remained and new questions emerged. Although the data are sparse I remained interested in examining the effect of the presence of calves on IFBF. As stated earlier, only three of the 40 cows were observed with calves. One lowland cow was observed with a single calf in fall, one lowland cow was observed with twins in fall, and one mountain cow was observed with a single calf in spring. Having determined the top model in the all subsets model selection (Table 2.4), I attempted to determine the importance of the variable presence of calf by comparing the top model to a new model created by adding the additive effect of presence of calf to the top model. Because information on calves were rare, I

created presence of calf as an indicator variable by combining fall and spring calf observations within individuals. This negated the information of the time of the observation (fall vs. spring) and number of calves, but was necessary due to the sparse data. Because information on presence of calf was not available for every individual each season creating the original top model and the presence of calf model would result in models created from different datasets and model comparisons would be illogical. Therefore, the original dataset was parsed so that only those individuals for which the variable presence of calf was recorded were included. AICc for the model with the presence of calf variable was 208.11 and 207.53 for the original model. Therefore, model selection provides marginal evidence that presence of calf is not an important variable. In addition, the parameter estimate for the calf variable has a 95% confidence interval that overlaps zero. Because gestation and lactation have such a profound influence on energetics (Schwartz and Renecker 1998, Parker et al. 2009), the vagueness of the analysis into energetics related to reproduction is probably due to the sparsity of the data. I speculate a larger sample size would have found the variable presence of calf to be an important determinant of IFBF.

I also questioned if the classification scheme used to create the factor levels for landscape type was optimal (Figure 2.2 and Table 2.2). Cows were grouped into landscape types according to the percentage of time they spent in each landscape. Another option is grouping cows into factor levels based upon the landscape type in

which they were originally captured. Comparisons of the original percentage of locations grouping model to the initial capture grouping model indicated that the percentage of time spent in each landscape type was the most appropriate classification scheme (percentage of time spent in each landscape type AICc = 252.41 vs. initial capture landscape type AICc = 253.95). After observing the raw data and model output (Figure 2.7) another option for a landscape type classification scheme is to create a new landscape factor level for migrant mountain moose. The new classification scheme would result in the three landscape factor levels lowland, migrant, and mountain. However, model selection indicated that the original two landscape types factor levels (lowlands and mountains) is more appropriate (two landscape types AICc = 252.41, three landscape types = 258.63). As with the presence of calf analysis, inferences into landscape factor levels are probably affected by the sparsity of the data and a larger sample size may have resulted in different conclusions. I also fit the top gls model to the measured MAXFAT values to obtain model-fit MAXFAT parameter estimates (Table 2.6).

2.5.5 Limitations and Recommendations

I chose to use IFBF estimates, rather than MAXFAT, because it provided a body condition measure that could be viewed in a much broader context across several species. However, using IFBF as the response variable requires additional work and a strong assumption. Because I used the Stephenson et al. (1998) regression to estimate the

response variable, I did not account for sampling variance associated with converting MAXFAT to IFBF and was forced to assume that there was no variation or insignificant variation in the relationship between IFBF and MAXFAT.

Elimination of the variable DMR from the analysis likely had little effect on the results because DMR and HRS were so highly correlated ($r = 0.87$). The high degree of positive correlation between HRS and DMR suggests that cows that move at a higher rate do so to access new areas (Chapter 3). Additionally, when making inferences into foraging activities it is not recommended to use time intervals greater than one hour, due to foraging bouts usually lasting less than one hour (Owen-Smith et al. 2010), and I was most interested in examining variation in DMR due to foraging activities . As demonstrated above, elimination of the variable presence of calf likely had little impact on the analysis because of the sparsity of the data. The observed low calf:cow ratio may be indicative of either low pregnancy rates resulting from a low bull:cow ratio, poor nutritional status of the entire population, and/or high predation rates. Wolves, black bear, and brown bear prey on moose in the study area.

The high degree of correlation between random effects may have caused issues for the lme and lmer models. High correlation of the random effects may cause numerical estimation problems (Pinheiro and Bates 2000, Crawley 2007, Zuur et al. 2009, Bates

2010) and may explain the model validation problems and wide confidence intervals observed in the lme models. Large confidence intervals on the standard deviations and correlation coefficient values near the boundaries (-1 and 1) may indicate the model is over-parameterized because the random effects covariance matrix is ill-conditioned (Pinheiro and Bates 2000). Correlation of random effects near the boundaries may indicate a singular matrix (Bates 2010). Despite heteroscedasticity and parameter estimation problems with the lme models, model selection of gls, lme, and traditional linear fixed effects resulted in the same top model and similar model rankings.

More tangible insight into wildlife-habitat relationships can be accomplished by incorporating a more resource selection-based design into the framework used in this study. A prime example is the resource selection method of Herfindal et al. (2009) that would also incorporate body condition or other fitness indicators. Future research would be much more informative if capable of relating body condition to movement and habitat at a finer resource selection scale than this study. The habitat data used in this study were forced to a very coarse scale (lowland vs. mountain) due to the small study sample size and great variability of moose habitat selection (Gillingham and Parker 2008). Future research in this area would benefit greatly by increasing sample size to determine how resource selection within and between landscape types affects fitness and energetics. This study's resolution of resource selection was limited by the small

unbalanced sample size (Table 2.2). By convention a sample size of ≥ 30 animals per group is required for resource selection studies (Leban et al. 2001).

Monitoring an entire year would also allow a more complete picture of energetics throughout all of the seasons. Monitoring for more than a single year would also allow estimation of the variation in energetics which is crucial as habitat conditions are dynamic. Also, cows were aged based upon body size and tooth wear observations in the field. I could have estimated age more accurately by collecting incisors for cementum annuli analyses (Schroeder and Robb 2005) to include age as a model covariate. Because I was interested in monitoring energetics during a single season I chose MAXFAT, but twinning rates (Franzmann and Schwartz 1985) and other more cumulative measures would be more suitable for annual or life-long studies. However, when using MAXFAT to make inferences into annual habitat quality, it is important to obtain MAXFAT measures when the animals are in their poorest body condition to ensure that the measures reflect the low in annual energy cycle for all animals so that all measure are directly comparable. E.g., for an annual habitat quality study of female moose it would not be as meaningful to compare say January MAXFAT measures, as it would be to compare repeated MAXFAT measures among individuals taken in both October and the following May. The later study design allows a more meaningful comparison because MAXFAT measures should be highest and lowest during those

sample times and the period of study will most accurately reflect annual fat use and differences in body condition.

MAXFAT is a good indicator of body condition when standardized for sex, age, body size, reproductive status, and time (Gustine et al. 2006, Cook et al. 2010). Cook et al. (2010) recommend combining MAXFAT estimates with body condition scores that are scaled for body mass. They demonstrated that positive bias results from measuring smaller sized animals and a negative bias results from measuring larger animals when MAXFAT is not scaled. Because moose have a much larger body size, bias is probably smaller than in deer or elk because the effect of allometric scaling is reduced in larger animals. In fact, Stephenson et al. (1998) did not use a scaling factor for adult cow moose across a broad range of body sizes and still observed a linear relationship between MAXFAT and IFBF. They did not find a relationship between the possible scaling factors total length and chest girth with body mass. They state that, "Within a single demographic group, other factors such as differences in fatness, pregnancy status, and quantity of digesta are more influential" (Stephenson et al. 1998:721). Therefore, the unscaled MAXFAT estimates I used are at least adequate for this study's objectives.

While Cook et al. (2010) state that MAXFAT analyses conducted by biologists with experience measuring MAXFAT are robust, they also suggest that MAXFAT alone is not a sufficient body condition measure in late winter/early spring. During this time, if

subcutaneous rump fat has been depleted and only fascia is reflected from the ultrasound, then MAXFAT values from three to zero mm indicate IFBF anywhere from 0% to 6%. Reclassifying cows with MAXFAT below three mm to zero mm and 5.6% IFBF had no influence on the analysis. I was fortunate to be able to use MAXFAT as a body condition estimate for all but one cow during spring measures (this cow had a MAXFAT measure of zero cm and was classified as 5.6% IFBF). The ability to use MAXFAT as a reliable body condition indicator was largely an artifact of the study monitoring period. All cows were in adequate body condition to have measurable MAXFAT. If I had taken measurements later in spring, it is probable that a larger proportion of MAXFAT measures would have been zero cm rendering vague IFBF values.

Because I used only MAXFAT, I was limited in the time I could accurately measure IFBF (not late spring). I recommend using body condition scoring in addition to MAXFAT estimates for studies that take measurements after early spring (Cook et al. 2010). This brings up the need for a moose body condition score that could be combined with MAXFAT similar to those created for mule deer and elk by Cook et al. (2010). I also recommend research into a scaling factor for MAXFAT in the future. If it is determined a scaling factor is required, it would be advantageous to have a scaling factor that is not biased by pregnancy status. Better yet would be a noninvasive metric such as those collected from urine or fecal samples. More information can also be gleaned by obtaining more frequent repeated MAXFAT measures on individuals. MAXFAT could

also be measured concurrent with age, pregnancy status, presence of calf in fall and spring, twinning rate, protein catabolism, body condition scores, and resource selection parameters to obtain a more detailed picture of the moose-habitat relationships. Similar to the ambiguities of defining availability in resources selection studies (Beyer et al. 2010), different home range models can lead to different conclusions concerning habitat quality (Mitchell and Powell 2008). In fact, HRS and overlap of Brownian bridge movement models, fixed-kernel density estimates, minimum convex polygons, and adaptive local convex hull models differed between individual cows of this study population (Chapter 3). I do not recommend using contiguous home range models (such as minimum convex polygons) to evaluate habitat relationships because they are not good at estimating areas used by animals, i.e., where feet actually hit the ground.

Biotelemetry technology, such as GPS and activity sensors, has contributed to a better understanding of wildlife space use and habitat relationships and certainly made this research possible. However, studies such as this could be more informative if supplemented with direct observations of wildlife to monitor habitat-related behavior. Direct observations lead to the most detailed information of behavior such as space use and resource selection (Kernohan et al. 2001). In addition, modeling behavior specific utilization distributions allows more direct inferences into why certain habitat relationships exist and how they may affect fitness. This allows researchers to determine the more important question of why a resource is used, as opposed to just

knowing if resource acquaintances have occurred, which may or may not be ecologically informative (Hundertmark 1998, Kernohan et al. 2001). The ability to create behavior specific utilization distributions, constructed from direct or indirect observations (Marzluff et al. 2001), coupled with models that simultaneously estimate home range and resource selection (Horne et al. 2008, Johnson et al. 2008) in a hierarchical framework (Gillies et al. 2006, Thomas et al. 2006) appears to be the next frontier in space use and resource selection studies.

2.5.6 Conclusion

I improved upon past research techniques by applying high resolution home range models in order to minimize bias associated with using contiguous home range models to examine space use-habitat relationships (Mitchell and Powell 2008). High resolution was achieved by using high-frequency GPS data to construct Brownian bridge movement models (Horne et al. 2007). I found differing energetic consequences of cow moose wintering in lowland and mountain landscapes by measuring IFBF late fall and early spring. By using body condition as an indicator of habitat quality, I found evidence to support the functional response of home range habitat selection (Mysterud and Ims 1998) within landscape type (second order selection), but not between landscapes. I did not find evidence to support the proposed negative relationship between HRS and habitat quality (Harestad and Bunnell 1979, Dussault et al. 2005b) during winter using

IFBF as an indicator of habitat quality. It is likely that the effects of moose reducing energy expenditure, an unproductive dormant season, and intra- and interspecific interactions during winter weakened the relationship. Ultimately, habitat quality is better defined in terms of fitness or body condition measures rather than space use parameters. Fitness and body condition measure realized habitat quality, while space use parameters may not always be related to fitness or body condition and are confounded by the functional response of habitat selection. I assume that for cow moose during winter habitat quality, which is determined by forage productivity, locomotion costs, thermal cover, hiding cover, and the spatial distribution of resources, is still important in determining potential home range size.

Combining the functional response of habitat selection (Mysterud and Ims 1998), and the home range size hypotheses (McNab 1963, Harestad and Bunnell 1979, McLoughlin and Ferguson 2000, Dussault et al. 2005b) with my findings, I amend the home range size to the space use hypothesis. I define this hypothesis as; space use is a functional response of the organism to the quality, abundance, and distribution of resources within the environment to acquire at least the minimum amounts of limiting resources in order to maximize fitness and energetics. This hypothesis is a useful model for describing and predicting the minimum area required by animals. In reality, space use will likely be larger due to intra- and inter-specific interactions, stochasticity in behavior, and the fact that animals are not aware of all the resources available to them.

Several researchers caution against the sole use of HRS as a measure of habitat quality or animal condition (Dussault et al. 2005b, Mitchell and Powell 2008, Linklater et al. 2010). My findings concur, for nonterritorial large mammal herbivores, such as moose, HRS alone is not a good indicator of habitat quality. The commonly held negative relationship may be theoretically justified for the quality of habitat potentially visited. Potential habitat quality provides a baseline for space use, but intra- and inter-specific interactions also play very important roles determining space use. In addition, the functional response of habitat selection at the home range scale (Mysterud and Ims 1998) supports the notion of animals increasing their HRS until at least the minimum amount of limiting resources are contained with the home range. Thus, it is expected that some animals with different HRS be in similar body condition. In practice small HRS does not result in good body condition and large HRS does not result in poor body condition (Figure 2.4).

Studying space use and fitness is a complex and difficult endeavor. They are systems ruled by behavior, heterogeneity, and chance. There are several routes for the animal to take that end with similar results and several similar routes that result in different ends. Space use and resource selection are linked processes determined by the state of the animal, the memory of the animal, and the habitat available. Knowledge of why animals use certain habitats is important to understanding ecological processes and implementing successful management programs (Hundertmark 1998, Marzluff et al.

2001, Dussault et al. 2005b). Combining body condition estimates with space use and habitat information can provide more tangible insights into wildlife-habitat relationships.

2.6 Figures

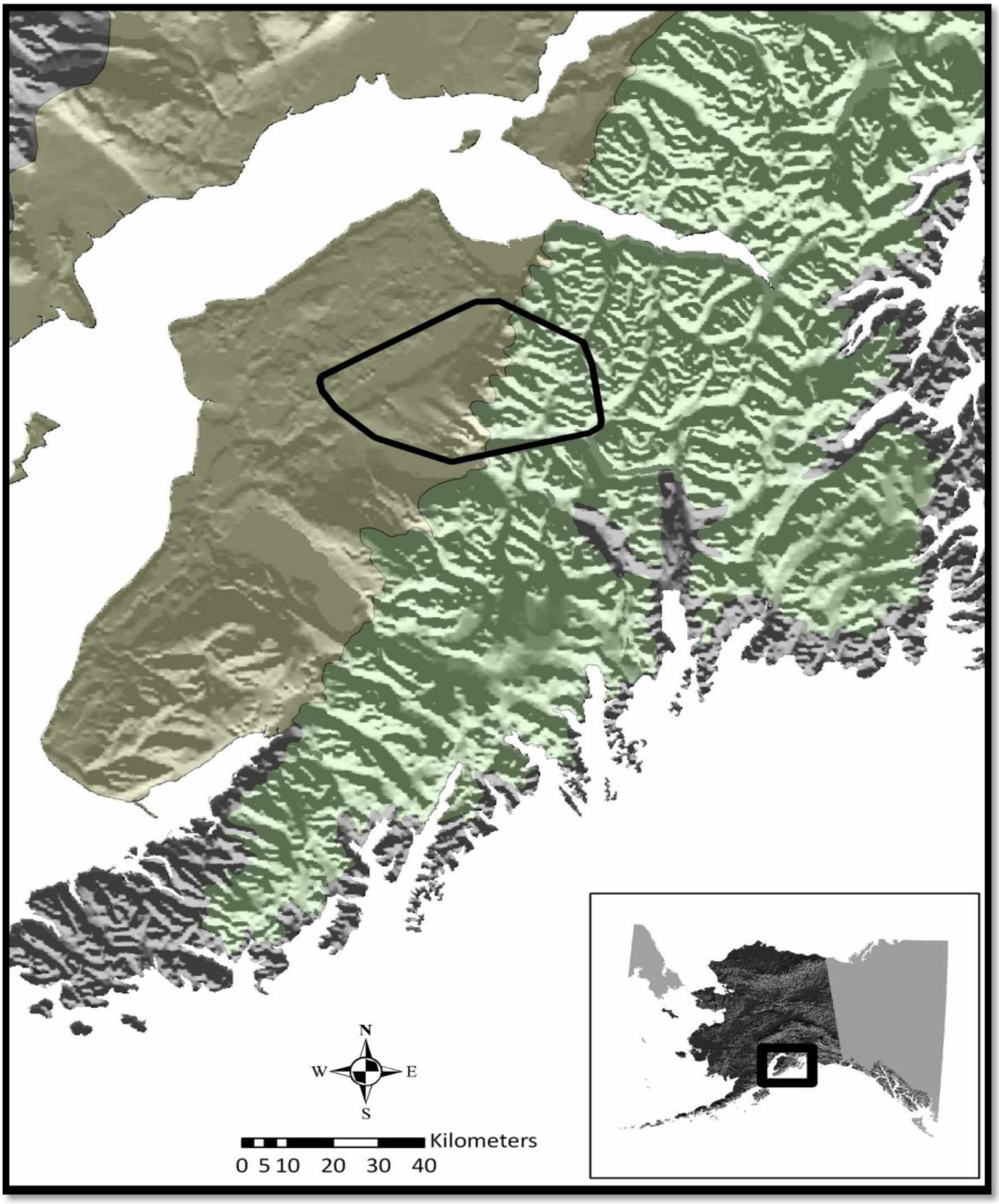

Figure 2.1. Map of the study area. The study area is located on the Kenai Peninsula, in south-central Alaska, USA. The black polygon demarcates study area; the black rectangle in insert demarcates the location of the Kenai Peninsula in relation to Alaska. Green areas represent mountains and brown areas represent lowlands.

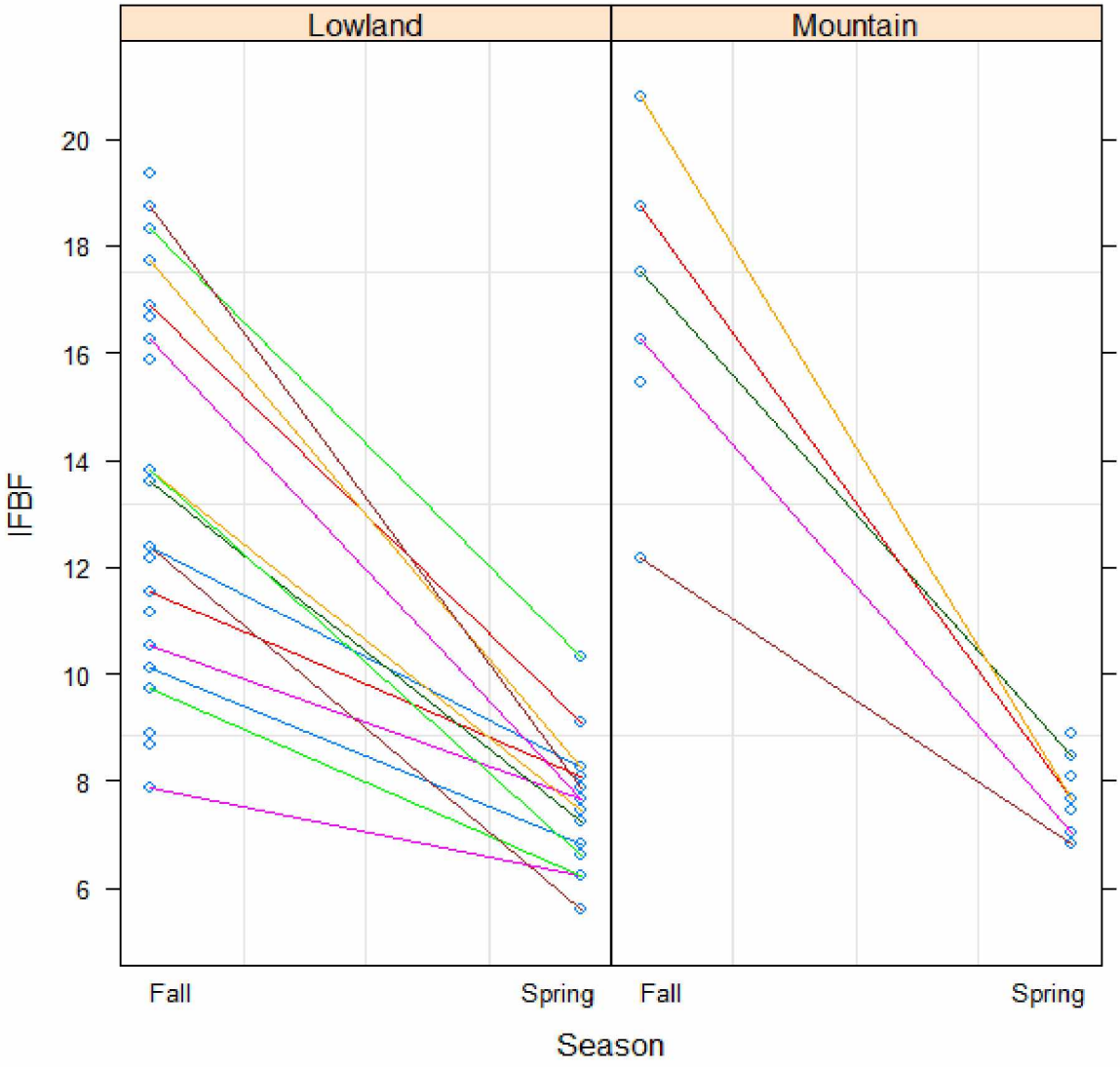

Figure 2.2. Ingesta-free body fat (IFBF) estimates. IFBF is estimated from rump-fat thickness (MAXFAT) ultrasound measures on adult cow moose inhabiting lowland and mountain landscapes on the Kenai Peninsula, Alaska, USA. Estimates were taken late November 2006 and early April 2007.

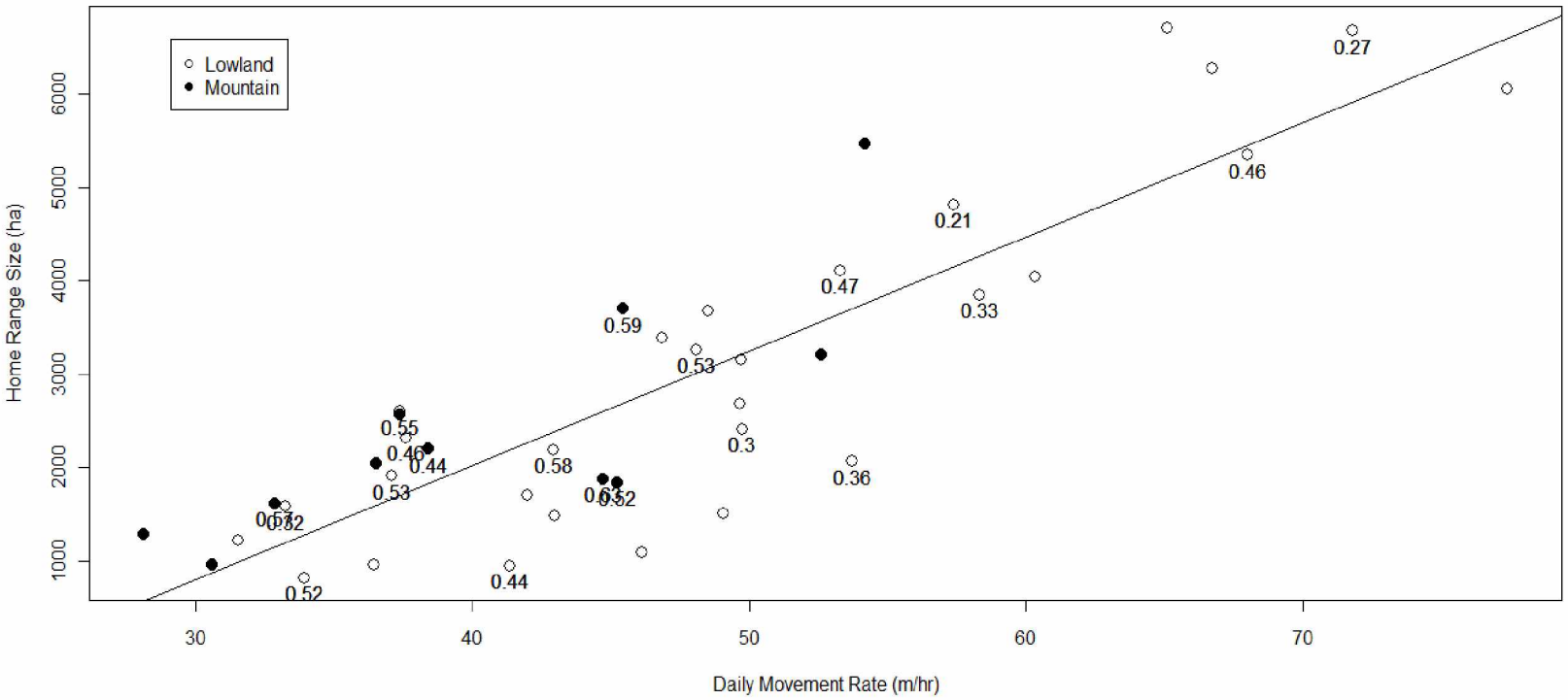

Figure 2.3. Home range size (HRS) vs. daily movement rate (DMR) and the percent of ingesta-free body fat (IFBF) used through winter. HRS (in hectares) as a function of DMR (in meters per hour) of adult cow moose in lowland (black circles) and mountain (black circles) on the Kenai Peninsula, Alaska, USA, during the 2006/2007 winter. Numbers under data points are the estimated IFBF use from fall 2006 to spring 2007. The black line is a least squares regression line constructed from all individuals. HRS was modeled using GPS location data and Brownian bridge movement models. DMR was estimated from two hour location intervals.

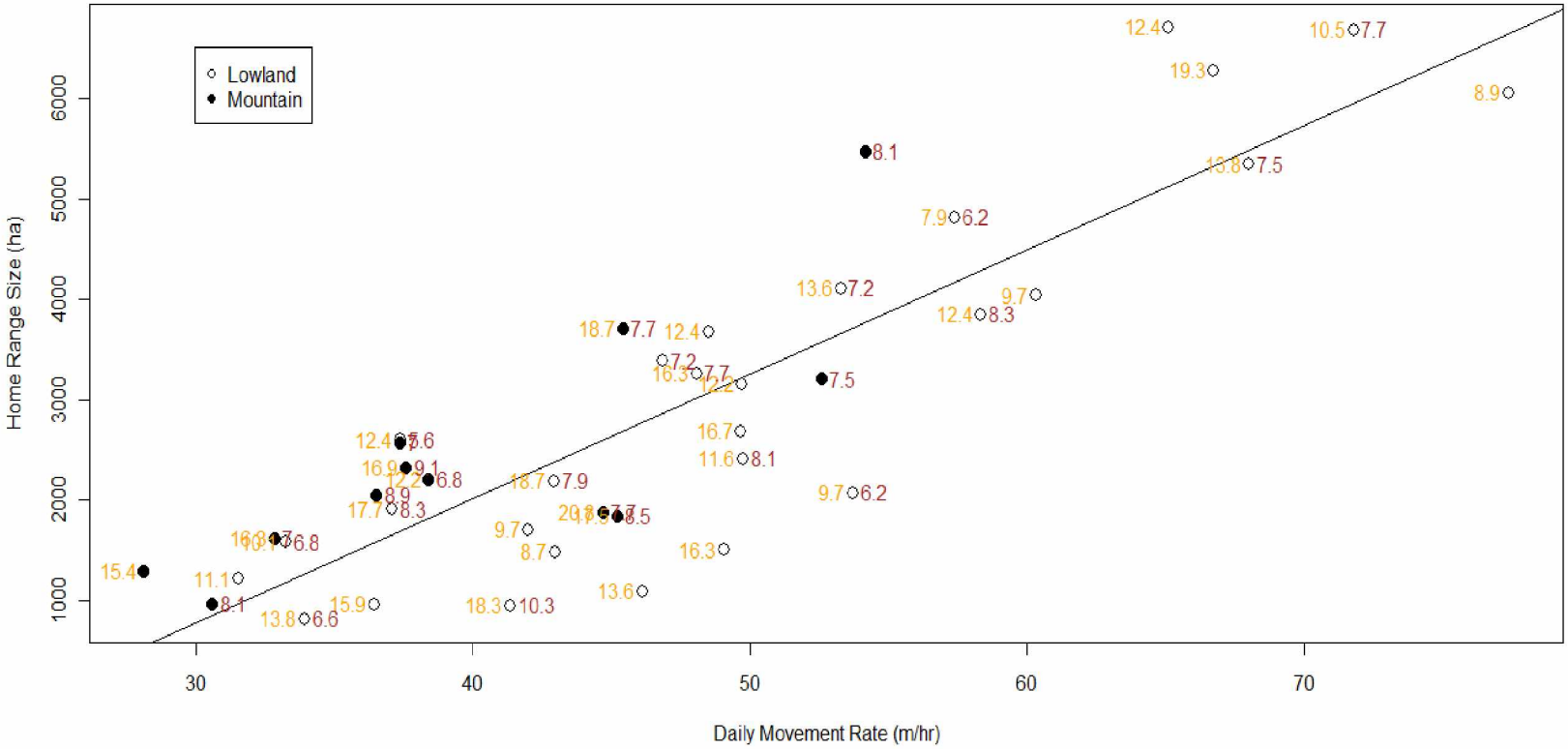

Figure 2.4. Home range size (HRS) vs. daily movement rate (DMR) and ingesta-free body fat (IFBF) values. HRS (in hectares) as a function of DMR (in meters per hour) of adult cow moose in lowland (black circles) and mountain (black circles) on the Kenai Peninsula, Alaska, USA, during the 2006/2007 winter. Numbers to the left of data points represent fall 2006 IFBF estimates and numbers to the right of data points represent spring 2007 IFBF estimates. The black line is a least squares regression line constructed from all individuals. HRS was modeled using GPS location data and Brownian bridge movement models. DMR was estimated from 2 hour location intervals.

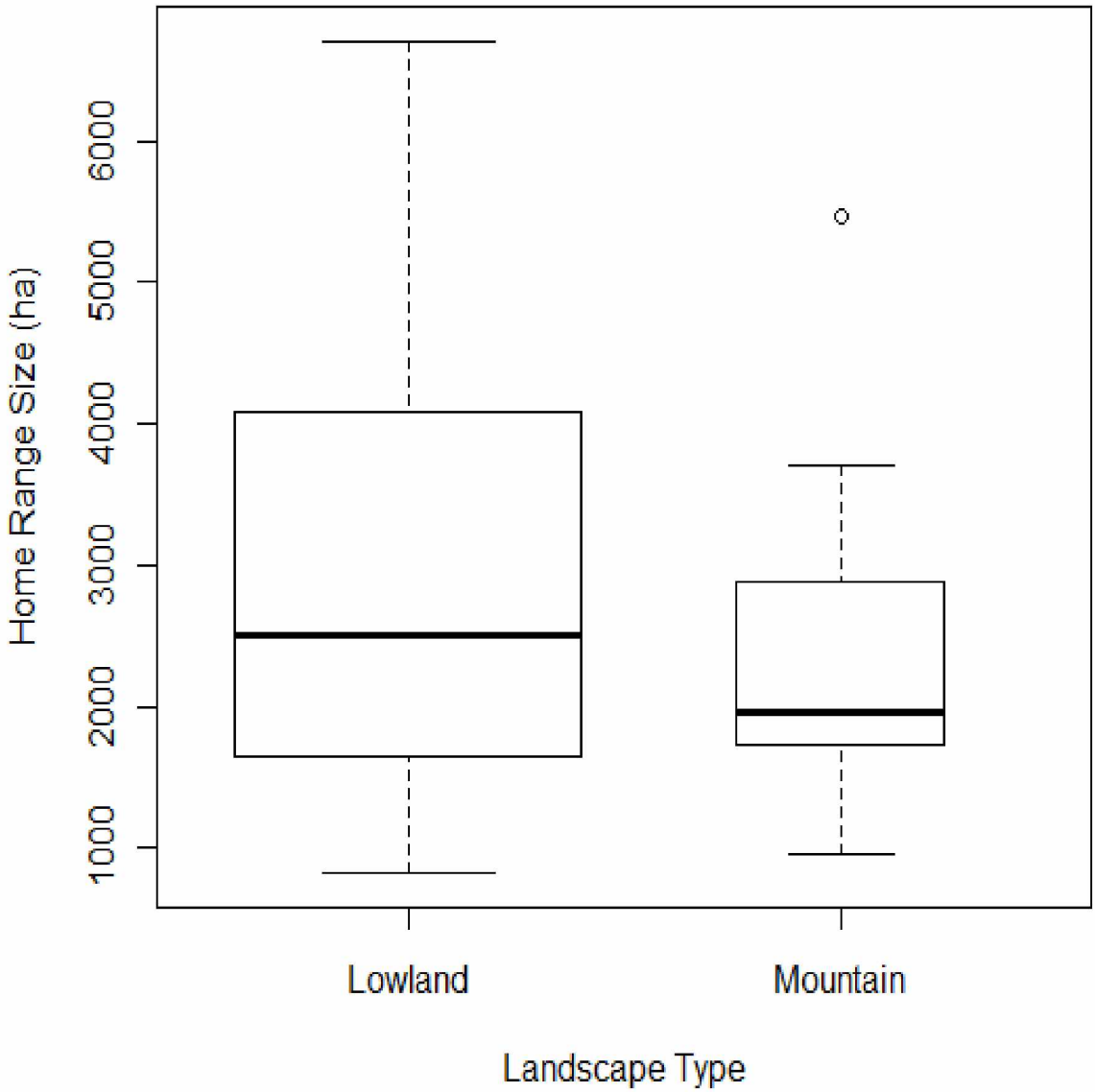

Figure 2.5. Home range size (HRS) as a function of landscape type. Plots of HRS as a function of landscape type used during the 2006/2007 winter of adult cow moose on the Kenai Peninsula, Alaska, USA. The width of the box-and-whisker plots is representative of the sample size (Lowland = 29, Mountain = 11).

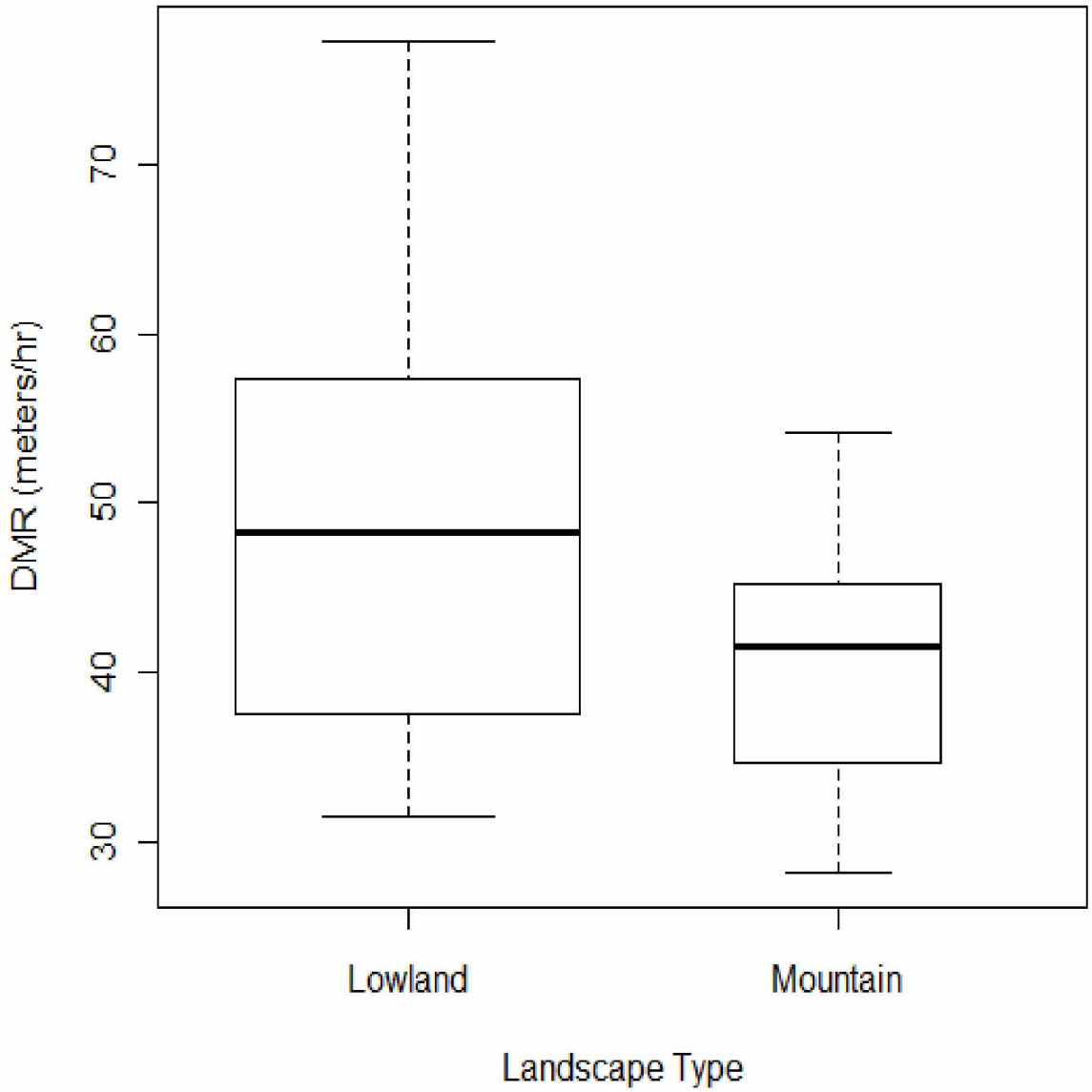

Figure 2.6. Daily movement rate (DMR) as a function of landscape type. Plots of DMR as a function of landscape type used during the 2006/2007 winter of adult cow moose on the Kenai Peninsula, Alaska, USA. The width of the box-and-whisker plots is representative of the sample size (Lowland = 29, Mountain = 11).

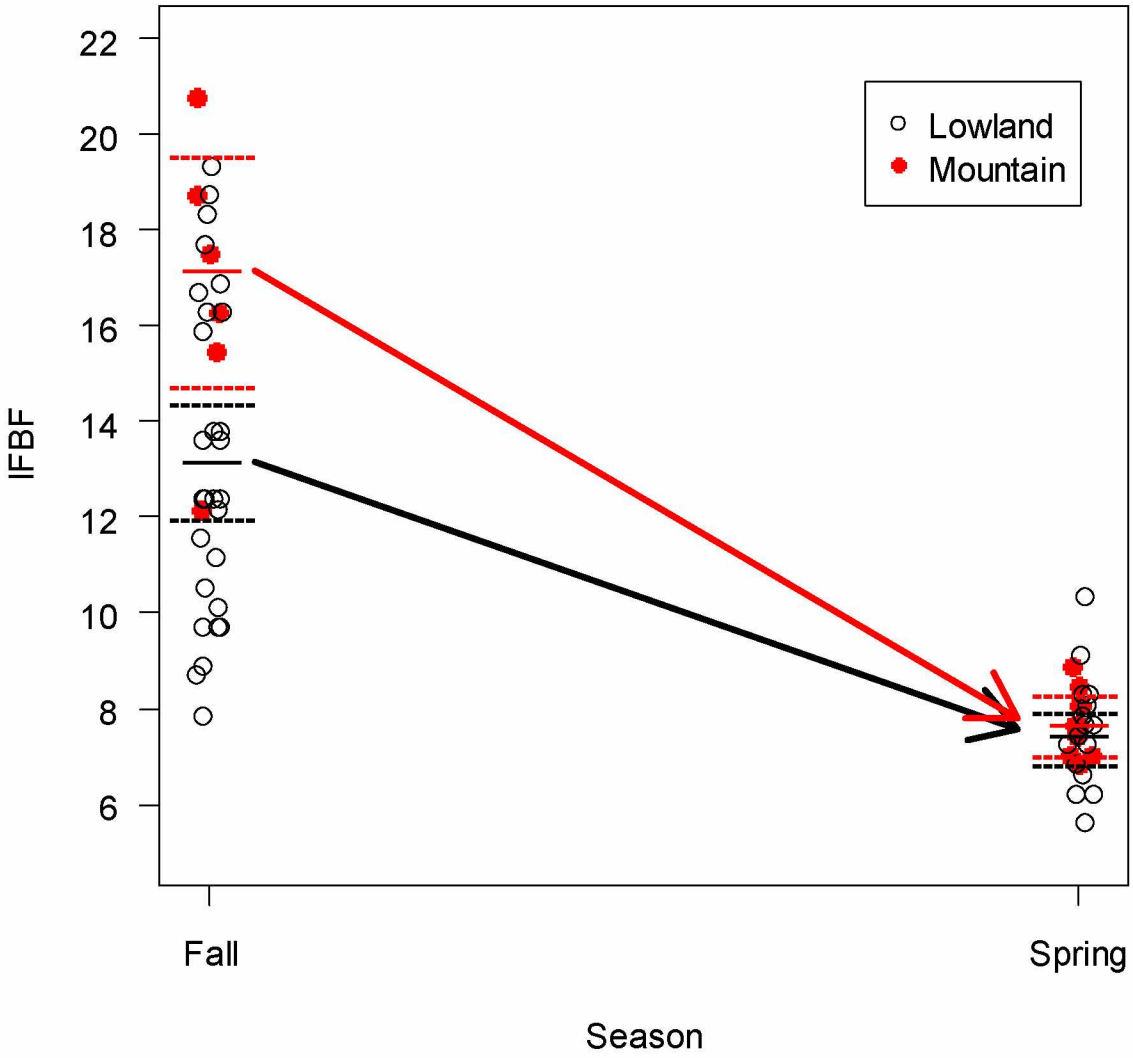

Figure 2.7. Model-fit and observed data of the percent of ingesta-free body fat (IFBF). Measures taken late fall 2006 and early spring 2007 on adult female moose on the Kenai Peninsula, Alaska, USA. Circles represent raw data values, solid lines are model-fit means, dashed lines are 95% confidence intervals, arrows point to transition means from fall to spring.

2.7 Tables

Table 2.1. Weather data. Weather data from Natural Resource Conservation Service SNOTEL stations from 12 November 2006 to 31 March 2007. The Moose Pens station is representative of the lowlands, while the Summit Lake station is representative of the mountains.

SNOTEL Station	Elevation	Mean daily low temp.	Mean daily high temp.	Mean snow depth	Initial snow depth	Final snow depth
Moose Pens	91 m	-15.9°C	-4.6°C	35.8 cm	12.7 cm	48.3 cm
Summit Lake	427 m	-16.8°C	-6.8°C	75.1 cm	15.2 cm	99.1 cm

Table 2.2. Sample size of the maximum depth of rump-fat thickness (MAXFAT) estimates. MAXFAT estimates taken late fall 2006, early spring 2007 on adult cow moose in the central Kenai Peninsula, Alaska, USA. MAXFAT estimates were measured by two researchers with a portable b-mode ultrasound.

	Landscape Type	
	Lowland	Mountain
Fall MAXFAT only	13	1
Spring MAXFAT only	1	5
Both Seasons	15	5
Total Sample Size	29	11

Table 2.3. Random error structure models. Rank of restricted maximum likelihood estimation repeated measures models to determine random error structure of the percentage of ingesta-free body fat of adult cow moose on the Kenai Peninsula, Alaska, USA during the 2006/2007 winter. The fixed effects landscape type, season, and home range size (HRS) and all interactions were included in the models. K-number of parameters, ΔAICc-is the difference of each model AICc value from the top model, w(i)-AICc model weight, Resid. LL-restricted log likelihood, lme-linear mixed effects model, gls-generalized least squares model.

Model	K	AICc	ΔAICc	w(i)	Res. LL
lme, random intercept and slope	12	317.28	0	0.46	-145.18
gls, correlation structure for measures within individuals, different variance structures for each season	11	317.86	0.58	0.35	-145.18
lme, random intercept and slope with different variance structures for each season	13	319.79	2.51	0.13	-145.18
gls, different variance structures for each season	10	323.24	5.96	0.02	-149.37
gls, variance structured by a power function of HRS for each season	11	324.25	6.97	0.01	-148.38
gls, variance structured by an exponential function of HRS for each season	11	324.81	7.53	0.01	-148.66
gls, different variance structured for each season and as a power function of HRS for each season	12	325.62	8.34	0.01	-147.49
gls, different variance structures for each season and landscape	12	326.93	9.65	0	-148.15
Random intercept model	10	344.15	26.87	0	-161.06
Traditional linear model	9	346.55	29.27	0	-162.47
gls, correlation structure for measures within individuals	10	346.62	29.34	0	-161.06
gls, different variance structures for each landscape	10	347.36	30.08	0	-161.44
gls, variance structured by an exponential function of HRS	10	349.16	31.88	0	-162.34
gls, variance structured by a power function of HRS	10	349.33	32.05	0	-162.42
gls, variance structured by a power plus a constant function of HRS	11	352.34	35.06	0	-162.42
gls, variance as a function of HRS	9	353.27	35.99	0	-165.83

Table 2.4. Fixed effects models. Rank of repeated measures models fit with maximum likelihood estimation to determine fixed effects of the percentage of ingesta-free body fat of adult cow moose on the Kenai Peninsula, Alaska, USA during the 2006/2007 winter. HRS = home range size, * indicates main effects and interaction terms, : indicates an interaction, + indicates an additive effect. Fixed effects are described in the text.

Model	K	AICc	ΔAICc	w(i)	LL
~ Landscape * Season	7	252.41	0	0.57	-118.13
~ Landscape + Season + HRS + Landscape:Season	8	255.05	2.64	0.15	-118.11
~ Season	5	256.20	3.79	0.09	-122.54
~ Landscape + Season + HRS + Landscape:Season + Season:HRS	9	257.05	4.64	0.05	-117.72
~ Landscape + Season + HRS + Landscape:Season + Landscape:HRS	9	257.81	5.41	0.04	-118.11
~ Season + HRS	6	258.56	6.15	0.03	-122.49
~ Landscape + Season	6	258.65	6.24	0.03	-122.53
~ Season * HRS	7	259.41	7.00	0.02	-121.63
~ Landscape + Season + HRS + Landscape:Season + Landscape:HRS + Season:HRS	10	259.93	7.52	0.01	-117.72
~ Landscape + Season + HRS	7	261.11	8.70	0.01	-122.48
~ Landscape + Season + HRS + Season:HRS	8	262.07	9.66	0	-121.62
~ Landscape * Season * HRS	11	262.34	9.93	0	-117.42
~ Landscape + Season + HRS + Landscape:HRS	8	263.70	11.30	0	-122.44
~ Landscape + Season + HRS + Landscape:HRS + Season:HRS	9	264.80	12.39	0	-121.60
~ Intercept only model (i.e., null model)	4	310.13	57.73	0	-150.70
~ HRS	5	311.99	59.58	0	-150.44
~ Landscape	5	312.43	60.02	0	-150.66
~ Landscape + HRS	6	314.43	62.02	0	-150.42
~ Landscape * HRS	7	316.84	64.43	0	-150.34

Table 2.5. Model fit percentage of ingesta-free body fat (IFBF) estimates. IFBF estimates of cow moose in during fall 2006 and spring 2007, Kenai Peninsula, Alaska, USA.

Landscape and Season	**mean**	**se**	**95% confidence interval**
Lowland Fall	13.21	0.60	12.01 - 14.42
Mountain Fall	17.17	1.20	14.77 - 19.57
Lowland Spring	7.48	0.23	7.02 - 7.94
Mountain Spring	7.69	0.31	7.06 - 8.31

Table 2.6. Model fit rump fat thickness (MAXFAT) estimates. MAXFAT estimates (cm) of cow moose measured in fall 2006 and spring 2007, Kenai Peninsula, Alaska, USA.

Landscape and Season	**mean**	**se**	**95% confidence interval**
Lowland Fall	3.71	0.29	3.12 - 4.30
Mountain Fall	5.64	0.58	4.47 - 6.81
Lowland Spring	0.91	0.11	0.69 - 1.14
Mountain Spring	1.01	0.15	0.71 - 1.32

2.8 References

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Chapter 3 Space Use Correlations and Home Range Model Comparisons of Female Moose during Winter[1]

3.1 Abstract

I observed a strong positive correlation between daily movement rate and home range size during winter in Alaska cow moose. This correlation implies that cows that move more often do so to access new areas and this results in home range expansion. To determine if the correlation was an ecological phenomenon or an artifact of using Brownian bridges movement models (BB) to model home ranges I evaluated the correlation with minimum convex polygons (MCP), fixed kernels (FK), and adaptive local convex hulls (LoCoH) models. The strong positive correlation with daily movement rate existed for all home range models except MCP. I also investigated home range size and overlap differences between the four home range models. Overlap is defined here as the intersection of two models divided by their union. All models differed in home range size estimates. MCP produced the largest home range size followed by FK, BB, and LoCoH. Overlap between home range models was most similar for BB vs. FK , followed by BB vs. LoCoH, FK vs. LoCoH, BB vs. MCP, MCP vs. FK and least similar for MCP vs. LoCoH. Overlap estimates between BB vs. MCP and FK vs. MCP factor levels

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were not statistically different. Contrary to previous mammal research, BB produced sensible home range estimates.

3.2 Introduction

I observed a strong positive correlation (r=0.87) between daily movement rate (DMR) and home range size (HRS) in cow moose (*Alces alces gigas*) during winter on the Kenai Peninsula, Alaska, USA (Chapter 2). Foraging ecology predicts such a correlation during periods when resources do not regenerate and are not productive such as winter or dry seasons (Owen-Smith et al. 2010). During those non-regenerative periods, animals consume seasonally nonrenewable resources in their immediate area and are then forced to expand their home range to acquire additional required resources. Forage, in particular, is a resource that induces such an ecological process. During periods of plant growth, forage regenerates and animals can remain in a certain area as long as production is greater than or equal to consumption. However, during the dormant season forage is not a renewable resource and consumption of forage results in depletion of preferred forage and forage patches forcing animals to move to new areas (with the exception that under conditions of extreme resource depletion over large geographic regions there is little benefit to moving; Owen-Smith et al. 2010, van Beest et al. 2010). Norwegian moose have been observed to have much lower site fidelity and more variable forage selection patterns during the winter, relative to the summer, due

to the depletion of forage resources resulting home range expansion (van Beest et al. 2010).

The home range models I constructed that detected the DMR-HRS correlation, Brownian bridge movement models (BB; Horne et al. 2007), use movement rate (i.e., motion variance) to calculate HRS. Therefore, it is expected that DMR will be correlated to HRS to a certain extent. I was not certain if the strength of the observed positive correlation (r=0.87) was an artifact of using BB or a true ecological phenomenon. It would be of value to evaluate if such a correlation exists using other popular home range models, so in addition to BB I used the three other contemporary home range models, minimum convex polygons (MCP; Mohr 1947), fixed kernels (FK; Worton 1989) and adaptive local convex hulls (LoCoH; Getz et al. 2007), to examine the DMR-HRS correlation. All of the home range models constructed use very different techniques to delineate animal home ranges. The models and their derivation are described below.

The BB are appealing for modern biotelemetry applications, such as global positioning systems (GPS), because they incorporate temporal correlation between point locations into the home range model (Horne et al. 2007). Scientific literature using BB to estimate home ranges is sparse, but BB were determined as poor for estimating badger home ranges (Huck et al. 2008). The BB are constructed by estimating an animal's movement path with three-dimensional bridges between consecutive locations as conditional

random walks (Brownian motion) that are estimated from the movement rate (motion variance) derived from the data. MCP have been, and continue to be, popular home range models (Millspaugh and Marzluff 2001, Laver and Kelly 2008, Nilsen et al. 2008). The MCP are constructed by connecting the outermost location points to form a single polygon. During the past two decades kernel density estimates, particularly FK, have been the most commonly used and discussed home range models (Millspaugh and Marzluff 2001, Fieberg 2007, Laver and Kelly 2008, Kie et al. 2010). The FK are constructed by combining bivariate normal distributions (i.e., kernels) that are positioned at each location point. A new method that has raised interest is local convex hulls and the recommended variant LoCoH. The LoCoH are a generalization of MCP (Getz et al. 2007) and are constructed by combining locations in close proximity to one another into hulls (i.e., subsets of MCPs). The above home range model types can produce very different home ranges (Figure 3.1).

Examining the DMR-HRS correlation with the aforementioned four home range models also raises the question of differences between the home range model types. There are a multitude of reviews on the differences between home range models, all of which provide sound advice (White and Garrott 1990, Millspaugh and Marzluff 2001, Huck et al. 2008, Laver and Kelly 2008, Mitchell and Powell 2008, Kie et al. 2010). However, these studies have not compared the four home range models BB, MCP, FK and LoCoH with field data collected from non-fossorial species.

Two simple metrics to compare home range models are HRS and the degree of spatial overlap between model types. HRS, as an area, provides a simple metric of the differences in magnitude between home range models, while overlap provides a metric on the similarity of the spatial distributions between two home range models.

This study has two objectives. The first is to verify that an observed strong positive correlation between DMR and HRS (Chapter 1) exists using four contemporary home range models. The second objective is to evaluate the differences among home range models in terms of HRS and overlap using data collected on free ranging animals in their natural environment.

3.3 Methods

The data used for this investigation are the GPS-collared cow moose from Chapter 1 with the addition of one other study animal. Thirty-one cows were captured and monitored from 12 November 2006 to 31 March 2007. Moose locations were stratified to the same two hour intervals (with the exception of four individuals that were stratified to two hour and twenty minute intervals). The GPS collars, data processing, and screening procedures are described in Chapter 1. All field and capture methods were approved by Alaska Department of Fish and Game, Animal Care and Use Committee, Assurance No. 06-03.

Home range models were constructed with three different software programs. The BB were constructed with the software Animal Space Use 1.3 (Horne and Garton 2009). Probability density grids were constructed in Animal Space Use. Grid extents were estimated as the greatest north and east location coordinates plus 700 m and the minimum south and west location coordinates minus 700 m. This ensured full coverage of the estimated utilization distribution. Maximum time intervals between locations used to estimate the utilization distributions ranged from 240 to 1121 minutes among individuals (mean = 472 minutes). Grid cell size was set to 25 m for all individuals. Grids were imported into ArcGIS (Environmental Systems Resource Institutem, 2009, ArcMap 9.2, ESRI, Redlands, California) as point features, converted to rasters, the rasters were then reclassified by grouping all valued cells into one class, then the reclassified rasters were converted to polygons using the simplified option. The FK were also constructed with Animal Space Use. Grids were constructed in Animal Space Use using likelihood cross-validation to derive the bandwidth (Horne and Garton 2006). Grids were then imported into ArcGIS. The same procedures used for BB were used for FK with the exception that grid cell size was not static, but based upon the individual grid cells sizes calculated in Animal Space Use. The MCP were constructed using the Home Range Tools extension for ArcGIS (Rodgers et al. 2007). The LoCoH models were constructed in ArcGIS with R software (R Development Core Team 2010) from a package developed by Getz et al. (2007). As recommend by the authors, the *a* parameter was estimated as the greatest distance between any two points within an individual's point pattern.

To evaluate the DMR-HRS correlations, correlation coefficients were calculated for DMR and HRS of each home range model. HRS estimates were calculated in hectares using 100% utilization distributions and all location points in the case of MCP. The DMR metric was defined as the mean three-dimensional distance moved, in meters, calculated at one hour intervals. Overlap was estimated as the area of intersection between two home ranges divided by their union (Figure 3.2). Overlap is a metric on a continuum between zero and one, zero indicating no similarity in the spatial distributions between two models, while one indicates equivalent spatial distributions between two models.

To estimate the difference between HRS and overlap between different home range models, HRS was modeled as a function of home range model and overlap was modeled as a function of home range model comparisons. The home range model comparisons consist of all possible combinations of overlap estimates between two models (e.g., BB vs. FK, MCP vs. LoCoH, etc,). Statistical analyses to estimate HRS and overlap differences were modeled via the protocol developed by Zuur et al. (2009). Using this protocol, statistical model selection based upon AICc (Burnham and Anderson 2002) was used to determine first the variance-covariance structure of the random error component followed by the fixed effects structure (see Chapter 2 for a more detailed description of the protocol). Tradition linear, generalized least squares, and linear mixed models were constructed to determine the random error structure. Deletion tests were used to

determine the importance of the fixed-effects factor levels (Crawley 2007). Deletion tests start by constructing the maximal statistical model (i.e., the model that includes all factor levels). Then a reduced statistical model is constructed by combining the two factor levels that are most similar. This reduced model is then compared with the maximal model using AICc. If the reduced model is best, then a new reduced model is constructed by combing two additional most similar factors levels (this can include the newly formed factor level). The new reduced model is then compared to with the former reduced model. This process is repeated until the model with more parameters is deemed better than the newly created reduced model. All statistical models were constructed in R software using aicmodavg (Mazerolle 2009) and nlme (Pineheiro et al. 2009) packages.

3.4 Results

There was a strong positive correlation between DMR and HRS with BB (r=0.87), FK (r=0.79), and LoCoH (r=0.86) home range models, but the correlation was not as strong for MCP models (r=0.55; Figure 3.3 and Table 3.1). Using model selection and adjusted r^2 values, the rank of home range model types at explaining variation in DMR were in descending order BB, LoCoH, FK, and lastly MCP (Tables 3.2 and 3.3).

The top model HRS model was a generalized least squares model with variance structured by home range model and symmetric correlation within individual moose that included all home range model factor levels (Tables 3.4 and 3.5). The mean HRS estimates were greatest for MCP (95% CI 5444-8470 ha) followed by FK (95% CI 2587-3923 ha), BB (95% CI 2355-3385 ha), and finally LoCoH (95% CI 1758-2689 ha; Figure 3.4 and Table 3.5). The top overlap model was a generalized least squares model with variance structured by home range model comparisons and symmetric correlation within individual moose that combined the model comparison factor levels BB vs. MCP and FK vs. MCP (Tables 3.7 and 3.8). Overlap estimates were most similar for BB vs. FK (95% CI 73-79%), least similar for MCP vs. LoCoH (95% CI 35-44%), and the same for the factor levels BB vs. MCP (95% CI 42-53%) and MCP vs. FK (95% CI 42-51%; Figure 3.5 and Table 3.8).

3.5 Discussion

This study illustrates the contrasting perspectives that may result when using different home range models to make ecological inferences, but confirms that a strong positive relationship between DMR and HRS exists during winter in cow moose. These findings confirm that when moose move more often during winter they do so to access new areas and this results in home range expansion. Three of four home range models indicated a strong positive correlation between DMR and HRS (Figure 3.2). This

confirms a principle in foraging ecology which asserts that home range is dictated by both the presence of resources and the regenerative capacity of those resources. It is predicted that during a nonproductive time, such as winter, animals must expand their home range to acquire the resources necessary for survival (Owen-Smith et al. 2010). In this study system it is likely that forage acquisition demands increase movement rate and drive home range expansion.

In addition to producing sensible home range estimates, BB are also good at comparing home ranges when models are constructed from location data using the same sampling interval . BB are also intuitively appealing. BB model autocorrelation that is inherent to location data and estimate the animal movement path (Horne et al. 2007). Estimating the movement path estimates the true process that generates location data. Animals create movement paths and interact with their environments in linearly. BB are also advantageous in that it is possible to model different behaviors resulting in different estimated path widths throughout the home range leading to models that more closely reflect reality. BB are also best at explaining the variation in DMR (Table 3.2), so in a sense you're getting two space use parameters when modeling with BB.

FK are advantageous in that they estimate the utilization distribution, but the issues of bandwidth selection (h) and smoothing still remain (Worton 1989, Horne and Garton 2006, Laver and Kelly 2008, Kie et al. 2010). However, in this study, FK and BB HRS and

overlap estimates were most similar. Advantages of LoCoH include estimation of the utilization distribution, capability to model sharp boundaries and gaps in home range, and the ability to use serially correlated data (Getz et al. 2007). Cons include the vague decision to optimize the *a* parameter value and need for a large sample size to converge to the true distribution.

I do not recommend MCP to estimate the area actually used by an animal. Although MCP are easy to construct, they positively bias HRS by including areas not actually used by the animal (Mitchell and Powell 2008), do not estimate home range boundaries well (Burt 1943), do not contain information on frequency of usage or internal structure of home ranges (i.e., the utilization distribution), and are sensitive to sample size (Börger et al. 2006). Burt (1943:351), having first defined the home range concept, called into question home range models such as MCP, "to connect the outlying points gives a false impression of the actual area covered. Not only that, it may indicate a larger range than really exists." MCP are not good at estimating areas used by animals, i.e., where feet actually hit the ground. Therefore, it is not surprising that MCP could not uncover the strong positive correlation between DMR and HRS. MCP may be useful in certain applications. MCP with external buffers may be applicable in resource selection studies as the area of available habitat or used for the construction of reserve boundaries.

My results contrast with those of Huck et al. (2008). They found that BB did not provide sensible badger home range estimates. I found that BB provided sensible moose home range estimates. Though the discrepancy between study results may be partially due to the use of different study animals, it is probable that other factors are also important. The difference in study results is likely due to Huck et al. excluding sedentary behavior at badger setts when calculating motion variance. The exclusion of sedentary behavior positively biased the estimated motion variance because only behavioral activities incorporating movement were used calculate the motion variance. Therefore, it is expected that their HRS estimates are positively biased and their need to use 40% isopleths to produce sensible home range estimates.

This study also demonstrates that location point patterns can influence HRS and overlap estimates among the four home range model types. MCP are very susceptible to the influence of point patterns. Aggregated J, L, C, and S-shaped point patterns show the greatest discrepancy in HRS and overlap between BB, FK, and LoCoH with MCP home range models, while more random point patterns result in similar HRS and overlap estimates among all home range models (Figure 3.6). I agree with Huck et al. (2008) that comparing home range models with data from study animals, as opposed to simulations, can provide judicious insights into home range model discrepancies. However, it would be valuable to conduct this study with simulated data to control for the influence of location point patterns on HRS and overlap estimates.

For future applications, I recommend the R package BBMM (Nielsen et al. 2010) to generate BB. Animal Space Use models generated were desirable, but took considerable computer time and required several data processing steps to create. The BBMM package appears more efficient at creating universally formatted files or shapefiles for ArcGIS. This raises another issue, the lack of a single software package capable of modeling current space use and resource selection techniques. Because there are several disparate software packages for space use and resource selection the choice of which model is applied is often biased by the researcher's knowledge of certain software programs. In practice this limits the applicability of new or more complex modeling. A platform for space use and resource selection software could be something in R and similar to program MARK (White and Burnham 1999). MARK has made great contributions to wildlife research and management via a convenient graphics user interface and highly usable platform for researchers of all statistical backgrounds. By focusing less on learning different software programs and the derivation of maths, researchers can concentrate more on the ecological aspects of research and maximize the already limited logistical budgets.

3.6 Figures

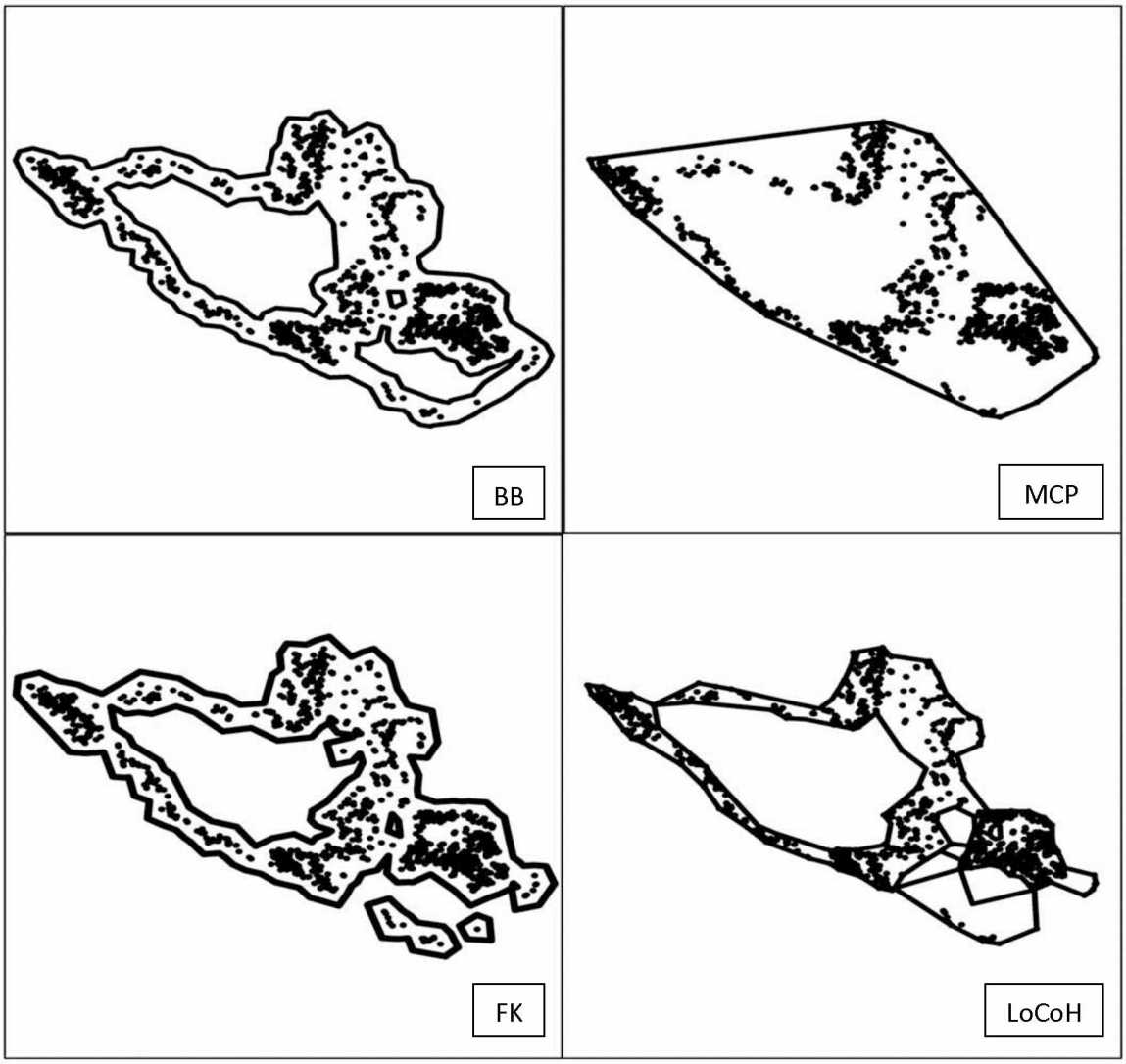

Figure 3.1. Four home range models. Four home range models estimated from field data from a single study animal. Home ranges were modeled as 100% utilization distributions and 100% of all location points using Brownian bridge movement models (BB), minimum convex polygons (MCP), fixed kernels estimated using likelihood cross-validation (FK), and adaptive local convex hulls (LoCoH).

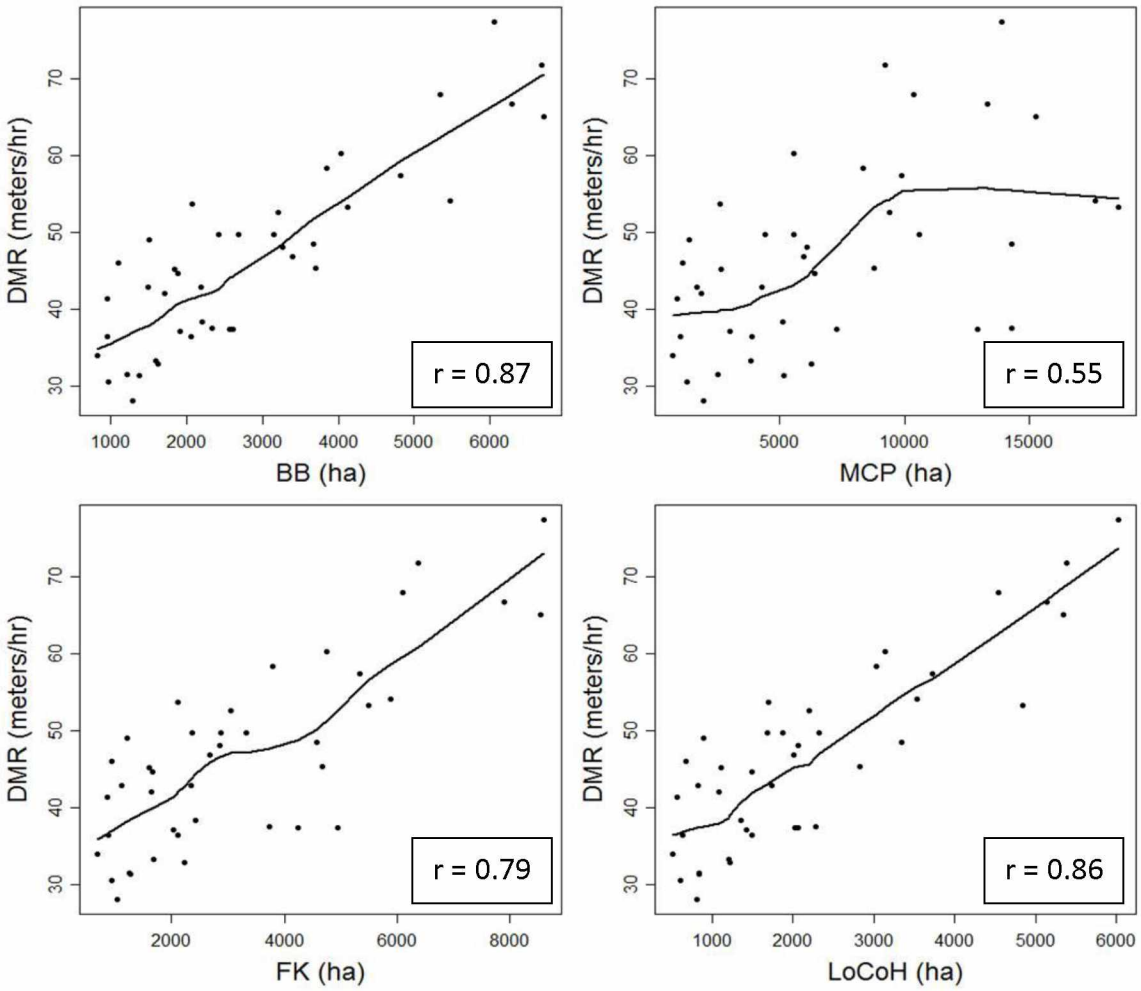

Figure 3.2. Scatter plots of daily movement rate (DMR) vs. home range size (HRS). Scatter plots of DMR vs. HRS in hectares (ha) for Brownian bridge (BB), minimum convex polygon (MCP), fixed kernels estimated using likelihood cross-validation (FK), and adaptive local convex hulls (LoCoH). LOESS smooth lines are fit to the data, r values indicate correlation coefficients.

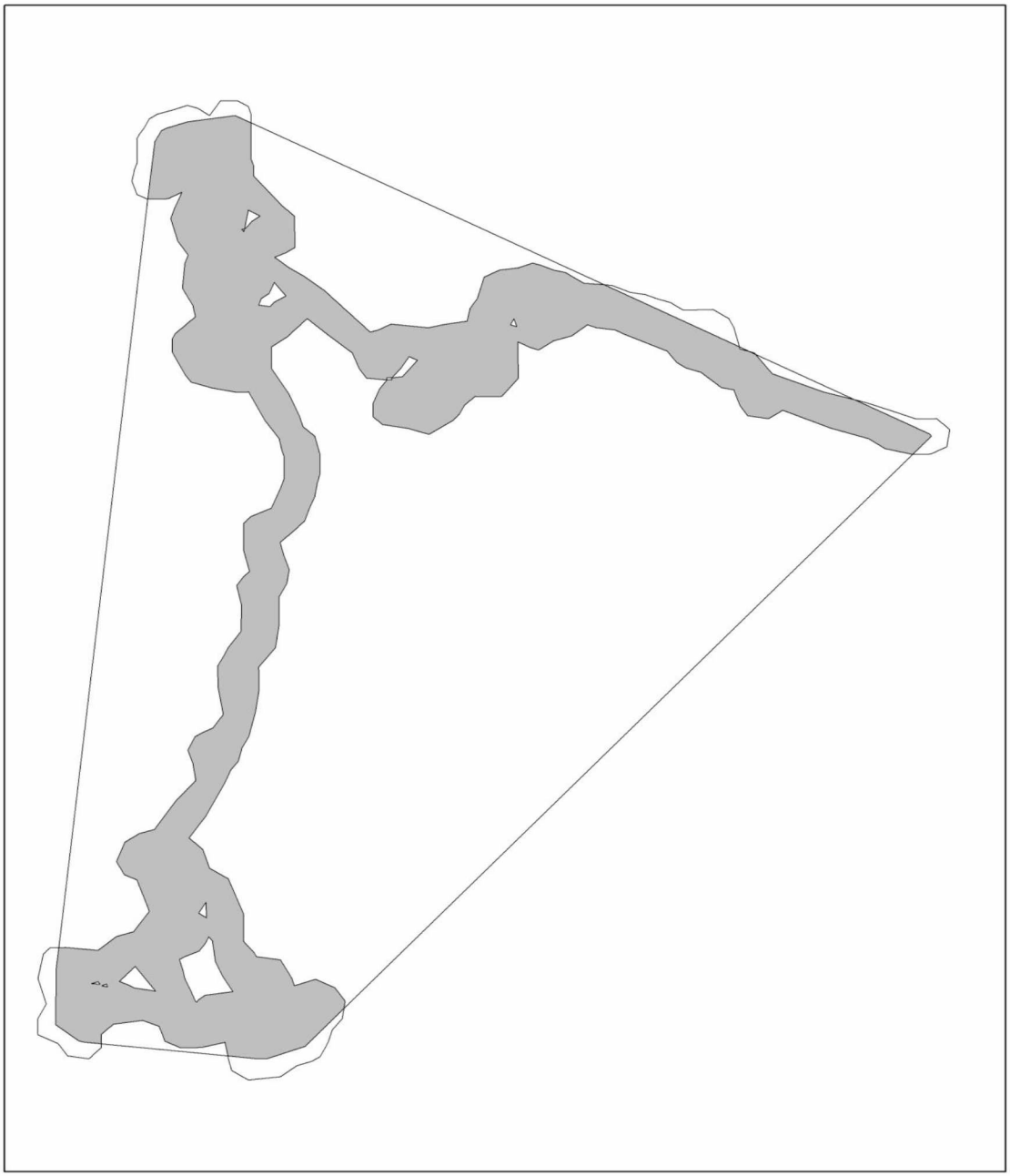

Figure 3.3. Derivation of the intercept metric. Image of Brownian bridge (BB) and minimum convex polygon (MCP) models from the same location data to illustrate the derivation of the overlap metric. The intersect is the area the two models have in common (the gray area). The intersect is divided by the union, which is the combined area of two models (the gray and white areas). This metric is zero when no spatial overlap occurs and one when the models overlap completely.

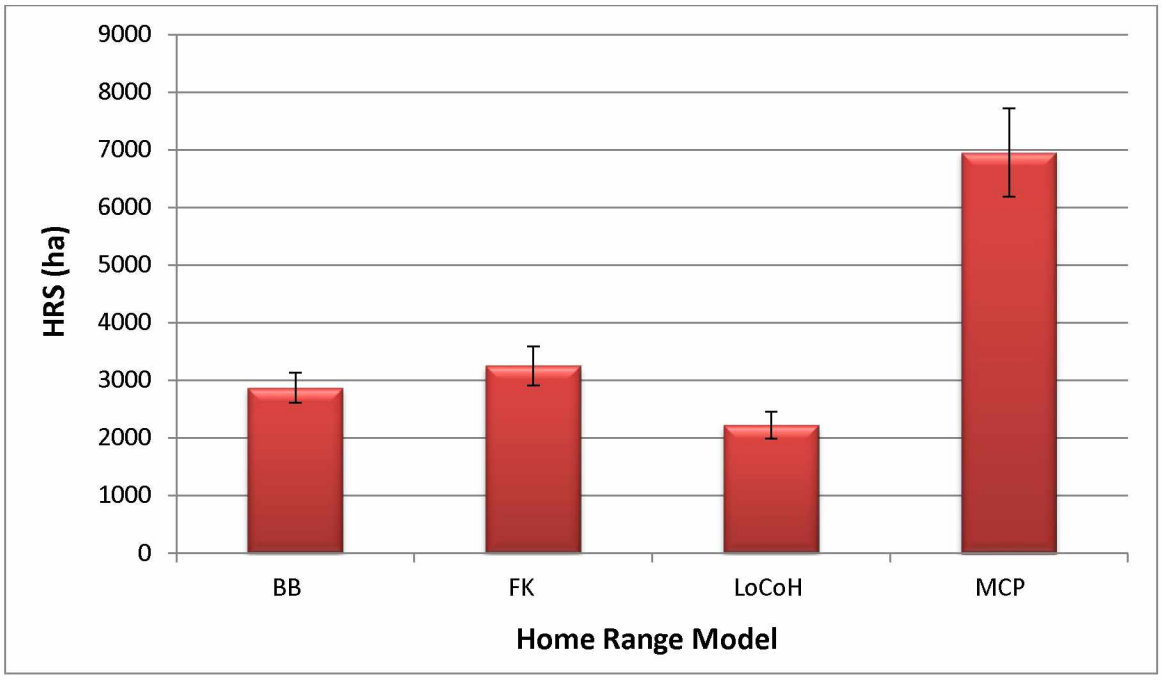

Figure 3.4. Mean home range size (HRS) estimates. Bar plot of mean HRS in hectares for Brownian bridge (BB), minimum convex polygon (MCP), fixed kernel (FK), and local convex hull (LoCoH) home range models. Error bars are one standard error.

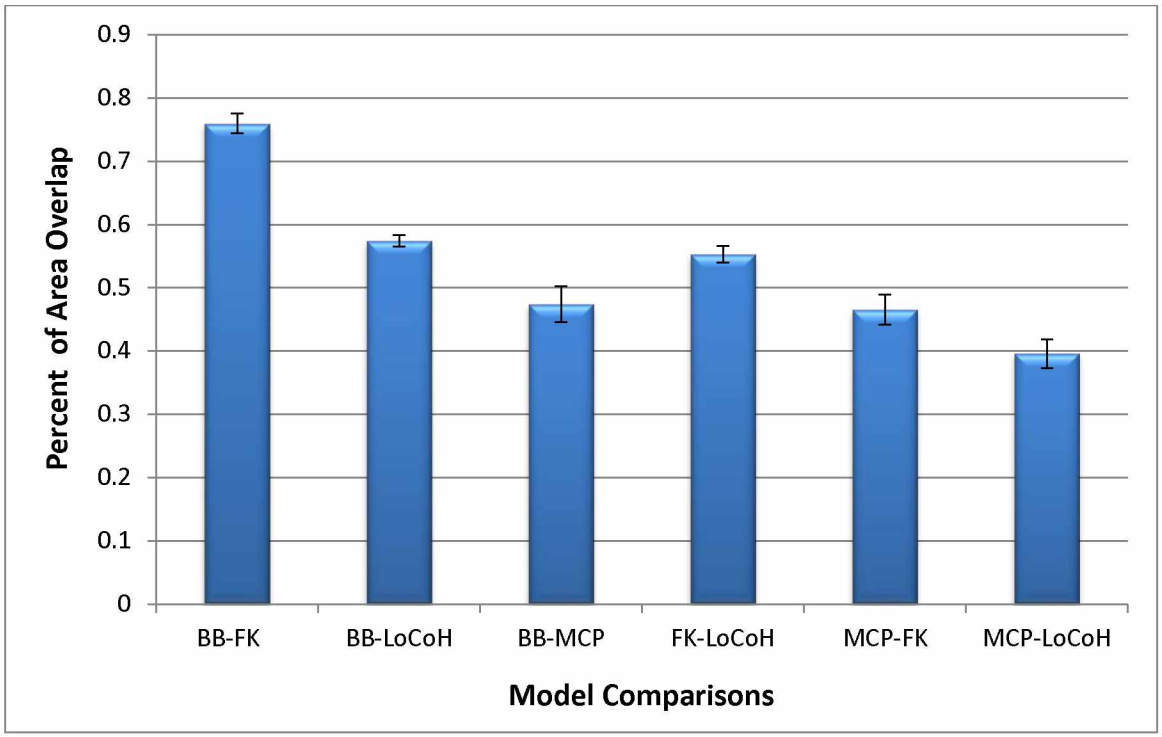

Figure 3.5. Mean overlap estimates. Barplot of the mean percent of overlap for Brownian bridge (BB), minimum convex polygon (MCP), fixed kernel (FK), and local convex hull (LoCoH) home range model comparisons. Error bars are one standard error.

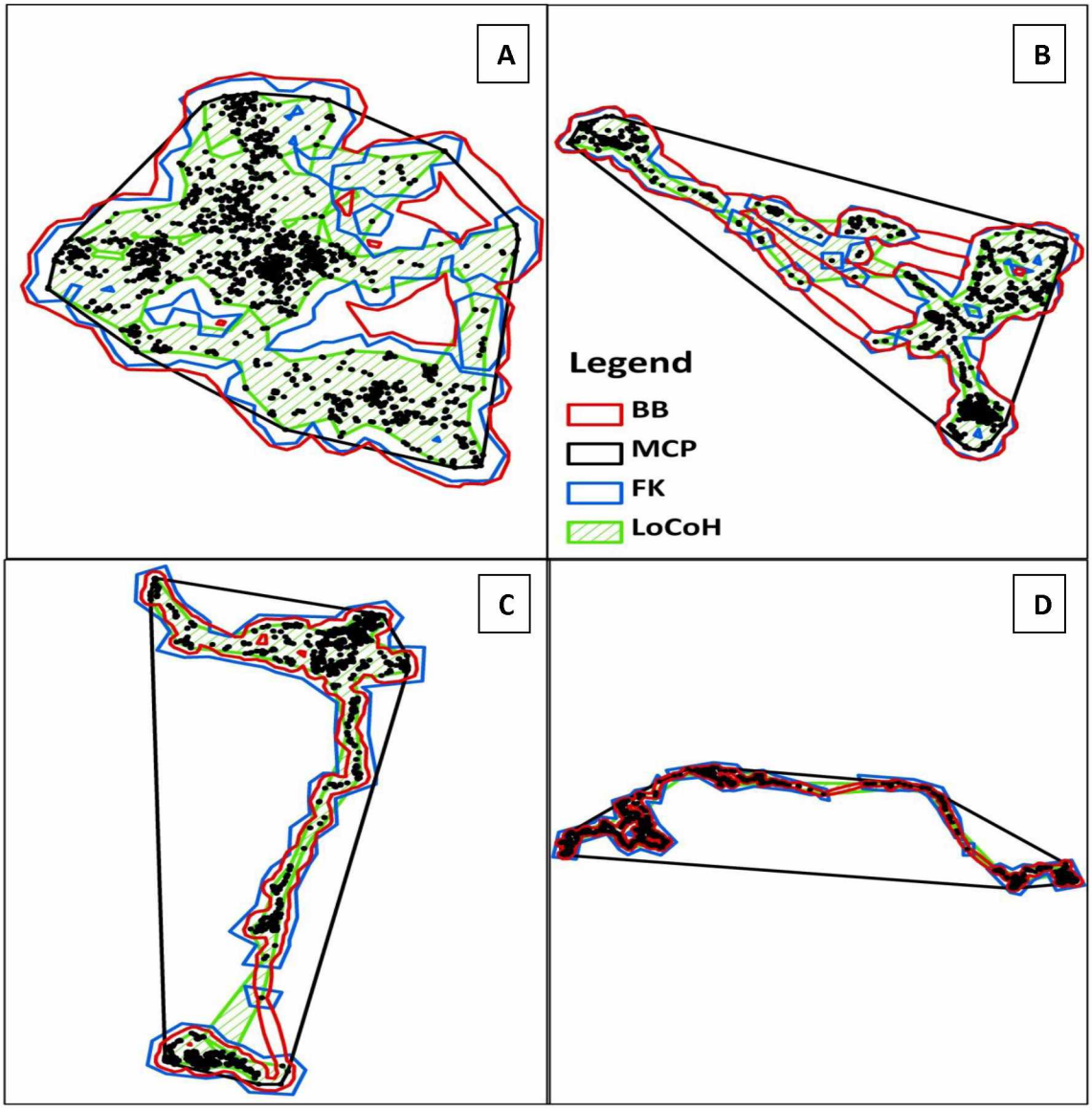

Figure 3.6. Point patterns, home range model, and parameter estimates. Brownian bridge (BB), minimum convex polygon (MCP), fixed kernel (FK), and local convex hull (LoCoH) home range models constructed from GPS data collected from four individuals with different point patterns. Home range size (ha) and overlap estimates (%) are A) HRS BB - 1503, MCP - 1415, FK - 1201, LoCoH - 898, overlap BB vs. MCP - 81, BB vs. FK - 80, BB vs. LoCoH - 60, MCP vs. FK - 72, MCP vs. LoCoH - 63, FK vs LoCoH - 68, B) HRS BB - 3386, MCP - 5995, FK - 2675, LoCoH - 2016, overlap BB vs. MCP - 50, BB vs. FK - 76, BB vs. LoCoH - 51, MCP vs. FK - 39, MCP vs. LoCoH -34 , FK vs LoCoH - 54, C) HRS BB - 1619, MCP - 6285, FK - 2227, LoCoH - 1225, overlap BB vs. MCP - 24, BB vs. FK - 66, BB vs. LoCoH - 60, MCP vs. FK - 21, MCP vs. LoCoH - 19, FK vs LoCoH - 47, D) HRS BB - 4040, MCP - 5598, FK - 4749, LoCoH - 3146, overlap BB vs. MCP - 15, BB vs. FK - 57, BB vs. LoCoH - 57, MCP vs. FK - 21, MCP vs. LoCoH - 16, FK vs LoCoH - 50.

3.7 Tables

Table 3.1. Correlation matrix. Correlation matrix of daily movement rate (DMR) and home range size (HRS) of Brownian bridge movement models (BB), minimum convex polygons (MCP), fixed kernels (FK), and local convex hulls (LoCoH) home range models.

	DMR	**BB**	**MCP**	**FK**	**LoCoH**
DMR	1	0.871706	0.547287	0.792022	0.860863
BB	0.871706	1	0.776965	0.951207	0.9659
MCP	0.547287	0.776965	1	0.839912	0.818562
FK	0.792022	0.951207	0.839912	1	0.964897
LoCoH	0.860863	0.9659	0.818562	0.964897	1

Table 3.2. Daily movement rate (DMR) as a function of home range size (HRS) for the home range models. Models of DMR as a function of home range size (HRS) of Brownian bridge movement models (BB), minimum convex polygons (MCP), fixed kernels (FK), and local convex hulls (LoCoH) home range models. K-number of parameters, ΔAICc-difference in AICc value from the top model, w(i)- AICc model weights, LL-log-likelihood, the number 1 represents the intercept or null model.

Model	**K**	**AICc**	**ΔAICc**	**w(i)**	**LL**	**Adjusted R^2**
DMR~BB	3	267.08	0	0.82	-130.22	0.7537
DMR~LoCoH	3	270.17	3.09	0.18	-131.76	0.7344
DMR~FK	3	285.11	18.02	0	-139.23	0.6177
DMR~MCP	3	310.98	43.89	0	-152.16	0.2816
DMR~1	2	323.24	56.16	0	-159.46	NA

Table 3.3. Home range size models variance-covariance structure of random error. Random error model selection based on AICc to determine home range size. K-number of parameters, ΔAICc-difference in AICc value from the top model, w(i)- AICc model weights, Res.LL-restricted maximum log-likelihood, gls - generalized least squares regression, lme - linear mixed effects.

Variance-covariance structure	**K**	**AICc**	**ΔAICc**	**w(i)**	**Res.LL**
Variance structure & symmetric correlation, gls	14	2707.4	0	0.58	-1338.29
Random intercept & slope, lme	15	2708.12	0.72	0.40	-1338.29
Random intercept, slope, & variance structure, lme	18	2714.79	7.39	0.01	-1338.29
Variance structure & compound correlation, gls	9	2755.9	48.5	0	-1368.36
Random intercept & variance structure, lme	9	2756.67	49.27	0	-1369.05
Random effects & variance structure, lme	6	2879.83	172.43	0	-1433.78
Variance structure, gls	8	2959.26	251.86	0	-1471.16
Random intercept, lme	6	2965.98	258.58	0	-1476.86
Variance structure by ID, gls	45	2983.26	275.86	0	-1429.09
Traditional linear model	5	3031.36	323.96	0	-1510.49
Random effects, lme	3	3106	398.6	0	-1549.96

Table 3.4. Home range size (HRS) fixed effects structure. Fixed effects model selection based on AICc to determine home range size. K-number of parameters, ΔAICc-difference in AICc value from the top model, w(i)- AICc model weights, LL-log-likelihood.

Factor Levels	**K**	**AICc**	**ΔAICc**	**w(i)**	**LL**
BB, MCP, FK, LoCoH	14	2755.04	0	0.97	-1362.11
BB and FK combined, others seperate	13	2761.74	6.7	0.03	-1366.66
FK and LoCoH combined, other seperate	13	2792.33	37.29	0	-1381.95
BB and LoCoH combined, others seperate	13	2799.47	44.43	0	-1385.52
All factor levels except MCP combined	12	2805.03	49.99	0	-1389.48
Intercept model	11	2809.5	54.47	0	-1392.88

Table 3.5. Home range size (HRS) estimates. HRS estimates and 95% confidence intervals for Brownian bridge (BB), minimum convex polygon (MCP), fixed kernel (FK), and local convex hull (LoCoH) home range models.

Home Range Model	**Lower 95% Interval**	**Estimate**	**Upper 95% Interval**
BB	2355.1	2870.15	3385.2
FK	2587.5	3255.3	3923.09
LoCoH	1758.36	2223.48	2688.61
MCP	5443.62	6956.96	8470.29

Table 3.6. Overlap models variance-covariance structure of random error. Random error model selection based on AICc to determine overlap. K-number of parameters, ΔAICc-difference in AICc value from the top model, w(i)- AICc model weights, Res.LL-restricted maximum log-likelihood, gls - generalized least squares regression, lme - linear mixed effects.

Variance-covariance structure	**K**	**AICc**	**ΔAICc**	**w(i)**	**Res.LL**
Variance structure & symmetric correlation, gls	27	-636.69	0	1	348.81
Variance structure & compound correlation, gls	13	-497.87	138.82	0	262.72
Variance structure, gls	13	-449.16	187.53	0	174.99
Variance structure by ID, gls	8	-419.72	216.97	0	219.88
Traditional linear model	12	-324.64	312.05	0	143.03
Random intercept & variance structure, lme	47	-322.98	313.71	0	237.96
Random intercept, lme	8	-293.55	343.14	0	218.01
Random effects & variance structure, lme	7	-271.59	365.1	0	154.92
Random effects, lme	3	-186.55	450.14	0	96.3

Table 3.7. Overlap fixed effects structure. Fixed effects model selection based on AICc to determine overlap. K-number of parameters, ΔAICc-difference in AICc value from the top model, w(i)- AICc model weights, LL-log-likelihood.

Fixed Effects	**K**	**AICc**	**ΔAICc**	**w(i)**	**LL**
BB vs. MCP and FK vs. MCP grouped	26	-684.63	0	0.69	371.52
All Levels	27	-683.04	1.59	0.31	371.99
BB and FK vs. MCP grouped and BB and FK vs. LoCoH grouped	25	-671.33	13.3	0	363.62
Intercept	22	-577.73	106.89	0	313.14

Table 3.8. Overlap estimates. Overlap estimates and 95% confidence intervals for Brownian bridge (BB), minimum convex polygon (MCP), fixed kernel (FK), and local convex hull (LoCoH) home range model comparisons.

Model Comparisons	**Lower 95% Interval**	**Estimate**	**Upper 95% Interval**
BB vs FK	0.73	0.76	0.79
BB vs LoCoH	0.56	0.57	0.59
BB vs MCP	0.42	0.47	0.53
FK vs LoCoH	0.53	0.55	0.58
MCP vs FK	0.42	0.47	0.51
MCP vs LoCoH	0.35	0.4	0.44

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Chapter 4 General Conclusion

This study examines moose energetics and space use during winter; a time of year considered critical because fitness factors tend to compound during this period (Parker et al. 2009). This study provides baseline information on moose-habitat relationships on the Kenai Peninsula in the face of a changing environment (Klein et al. 2005).

I found differing energetic consequences for moose wintering in lowland and mountain landscapes on the Kenai Peninsula. Mountain moose had a higher percentage of body fat in fall, but used these reserves at a faster rate through winter resulting in similar body fat estimates for lowland and mountain moose in spring. Therefore, it appears lowlands were of higher habitat quality during the study period. However, because this study is based on a single season, it is not certain if the observed landscape type-habitat quality comparison is static.

Using the percent of body fat as an indicator of habitat quality, I was also unable to find evidence of the proposed negative correlation between home range size and habitat quality (Harestad and Bunnell 1979). I did find evidence of the functional response of habitat selection at the home range scale (Mysterud and Ims 1998) in that moose of similar body condition had home range sizes spanning the observed range of home

range size estimates. Therefore, home range size alone is not a good indicator of habitat quality in this system.

A strong positive correlation between home range size and daily movement rate existed for Brownian bridge (Horne et al. 2007), fixed kernel (Worton 1989), and local convex hull (Getz et al. 2007) home range models, but was marginal for minimum convex polygons (Mohr 1947). Home range size estimates differed for all four model types. Overlap estimates differed for all but Brownian bridges vs. minimum convex polygons and fixed kernels vs. minimum convex polygons model comparisons. Brownian bridges provided sensible home range estimates and valid home range size comparisons. The successful application of Brownian bridges was largely due to the use of the same sampling interval on location data for each observational unit (study animal). Applications of minimum convex polygons should be evaluated thoroughly. This home range model may not be good for estimating home ranges, but could be useful when combined with an external buffer for defining available areas in resource selection studies or refuges and sanctuaries.

Space use and resource selection are linked processes determined by the state of the animal, the memory of the animal, and available habitat. This study illustrates the complexity of studying animal behavior in their natural habitats. It is a difficult, but

rewarding endeavor that provides sound knowledge of ecological processes which can aid management programs.

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